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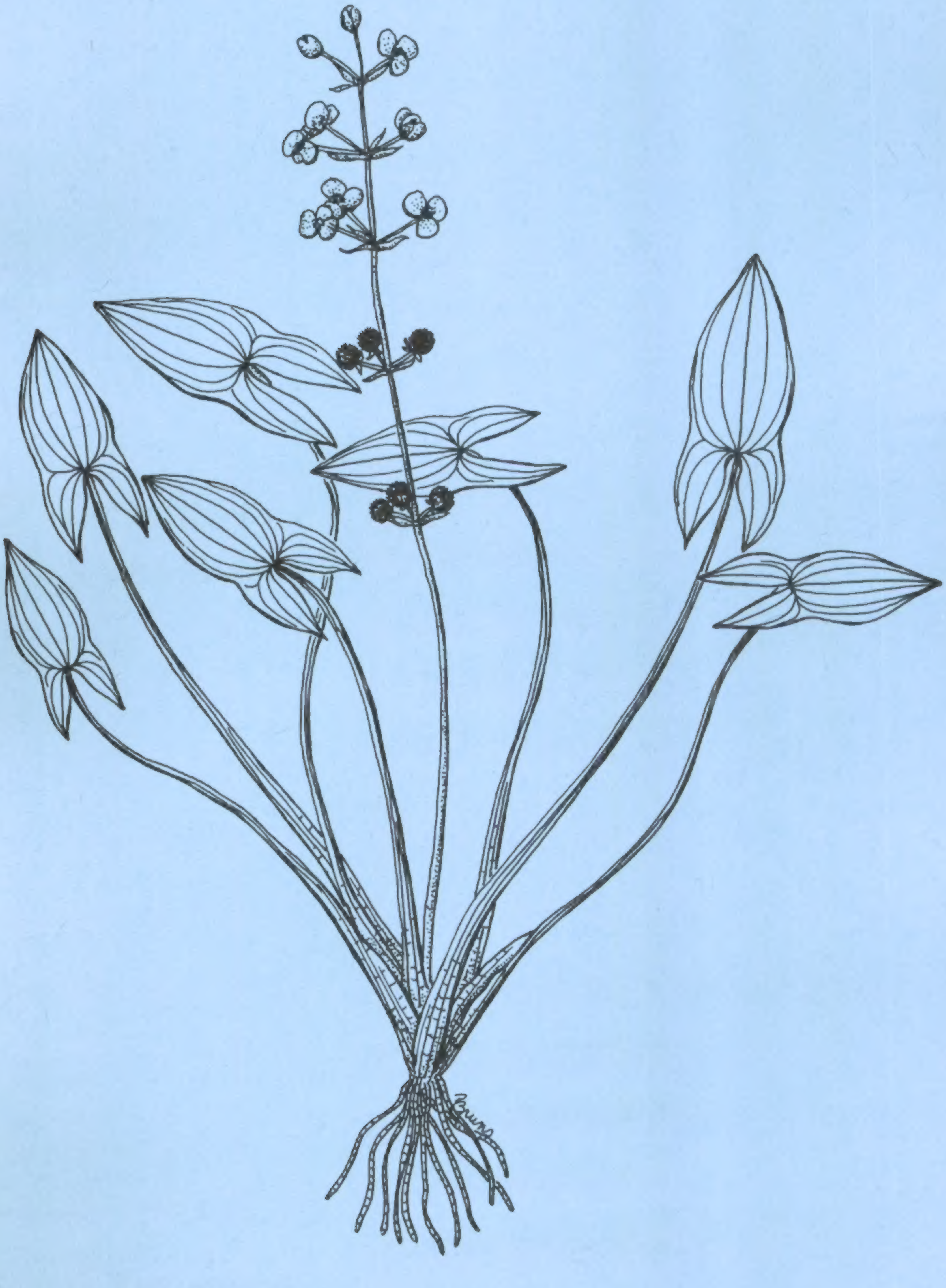

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Cover illustration

Sagittaria cuneata, a northern species, is fairly common in northern New England, rarer to the South except down the Rockies. The species is variable, often producing flat, linear leaves similar to *Vallisneria americana* when growing submerged in rivers.

Original art by Pamela Bruns, reprinted here by permission from Hellquist, C. B., & Garrett E. Crow, *Aquatic Vascular Plants of New England. Part 3. Alismataceae,* New Hampshire Agr. Expt. Sta., UNH, Durham, N.H.

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A MONOGRAPH OF THE GENUS MALVASTRUM A. GRAY (MALVACEAE: MALVEAE) [1,2]

STEVEN RICHARD HILL[3]

ABSTRACT

Malvastrum, a genus of yellow-flowered annual or perennial tropical and subtropical herbs in the Malvaceae, was described by Asa Gray in 1849 to include members of *Sida* and *Malva* that did not quite fit into those genera. During the next century the rather ill-defined genus became a repository for over 300 names. Subsequent monographic work brought about refinements in its circumscription that resulted in generic segregates and a core of so-called "true" Malvastrums. After morphological, karyological, phenological, and numerical analyses, the present study accepts seven sections, 14 species, six subspecies, and two varieties in *Malvastrum.*

The following contributions have been made: 1) the citation of all of the names published in *Malvastrum* together with their present placement and disposition of types; 2) an analysis of the geographic distribution of *Malvastrum* together with an hypothetical account of the origin and subsequent dispersal of the species; 3) a comparison of the morphology, chromosome numbers, limited hybridization data, and floral behavior within *Malvastrum* resulting in a proposal of infra- and intergeneric relationships; 4) the inclusion of a revised generic description and diagnostic key to the taxa; and 5) the inclusion of a detailed description, synonymy, and illustration for each taxon, several of which have never previously been illustrated.

The Malvaceae, placed within the order Malvales, is a moderately large family of flowering plants occurring throughout the tropical

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[1]Submitted to the Department of Biology, Texas A & M University, College Station, Texas, in partial fulfillment of the requirement for the degree of Doctor of Philosophy.

[2]Editor's note: This is part one of three. Part II, including much of the Taxonomic Treatment, and Part III, concluding the Taxonomic Treatment and including the appendixes and all references, will be published in Vol. 84, No. 838 (April) and Vol. 84, No. 839 (July), respectively.

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and temperate regions of the world but with its greatest diversity in the American tropics. Composed of more than 1500 species, the family is characterized by alternate and usually primarily palmately-veined leaves with well-developed but occasionally deciduous stipules, a superior ovary with generally three to ten or up to an indefinite number of carpels, an actinomorphic corolla with usually clawed asymmetric distinct petals united to the stamen tube, an androecium composed of monadelphous stamens with mostly unilocular anthers bearing echinate pollen, and by capsular, baccate, or schizocarpic fruits. The family is currently subdivided into five tribes: Gossypieae, Hibisceae, Decaschistieae, Malvavisceae, and Malveae, characterized by differences in the fruit type, the number of carpels, the degree of connation of the styles, the ratio of style to carpel number, the characteristics of the apical region of the stamen tube, and by the presence or absence of gossypol glands. Of these five tribes, the most species-rich and also one of the least understood is the tribe Malveae. This diverse tribe can be distinguished from the other four by the lack of apical teeth on the stamen tube, by its schizocarpic or pseudo-capsular fruits consisting of rarely one or two, usually three to many carpels, by the styles which are apically free at least one-fourth their length, by the ratio of one style per carpel, and by the lack of gossypol glands. Revisionary work within this tribe has been rapid in the last decade, increasing the number of its accepted genera from 53 (Bates, 1968) to the present total (1979) of 65.

The genus *Malvastrum* was described in 1849 by Asa Gray. His original intention was to segregate out certain members of *Sida* and *Malva* to leave those two genera more "natural" and clearly defined. The generic characters that he used to circumscribe *Malvastrum* were later found to encompass several otherwise dissimilar groups of species, and so *Malvastrum* became an artificial assemblage. During subsequent years over 300 names were published in *Malvastrum*. Major assemblages of related species have previously been removed into previously published genera or have been given generic status (particularly the genera *Acaulimalva* Krapovickas, *Anisodontea* Presl, *Malacothamnus* Greene, *Monteiroa* Krapovickas, *Nototriche* Turczaninow, *Tarasa* Philippi, and *Urocarpidium* Ulbrich). Revisions of these genera have left the remaining true Malvastrums without a complete treatment, and that has been the subject of the present study.

Taxonomic decisions have been based upon herbarium specimens examined at and loaned by the major domestic and foreign herbaria, upon examinations of locally cultivated individuals of most of the taxa, and upon field observations of the three Malvastrums in Texas. During this examination, the morphological characters of the specimens were recorded and compared, karyological preparations were made, and the phenology of living individuals was studied. After the range of variation in the samples had been determined, a numerical analysis was undertaken to aid in constructing relationships among the taxa. The result has been to accept seven sections, 14 species, six subspecies, and two varieties in *Malvastrum*.

Taxonomic and nomenclatural order has been brought to the five most variable species or species-complexes. The exceedingly variable *Malvastrum bicuspidatum* in Mexico has been divided into four well-defined subspecies and one additional variety, the subspecies corresponding to major geologic subdivisions of that region. Evidence is presented that suggests that *Malvastrum corchorifolium* is an allopolyploid (octoploid) derivative of the tetraploids *M. americanum* and *M. coromandelianum*. The variable *M. tomentosum* in South America has been divided into two geographically and morphologically distinct subspecies. The variation in *M. americanum* in Australia is interpreted to have resulted from a long history in that region, and one distinctive new variety is included. Finally, *M. coromandelianum* has been divided into three subspecies that are morphologically, geographically, and phenologically isolated from one another.

As a result of this study, *Malvastrum* is now considered to be a small, clearly defined, mostly American genus with 14 species, and is considered to be isolated from all of the other genera in the tribe Malveae (Malvaceae) but with probable affinities with the larger *Abutilon* alliance.

ACKNOWLEDGMENTS

I wish to express my gratitude to Dr. Paul A. Fryxell, whose continued support and generous sharing of his time, equipment, facilities, and specimens have made this study possible.

I am indebted to Ing. Antonio Krapovickas of the Facultad de Agronomía y Veterinaria, Corrientes, Argentina, for a very helpful

reply to a series of questions concerning European type materials. I am also indebted to Dr. Hugh Wilson of Texas A & M University for obtaining and providing me with photographs of the Philippi type specimens at Santiago, Chile (SGO).

Many members of the curatorial staffs of herbaria in the United States and Europe have been particularly helpful in providing information and specimens necessary for this study. Herbaria cited in this study follow the acronyms of the Index Herbariorum (Holmgren & Keuken, 1974) with the exception of Fryxell's research herbarium (pf) and my own research collection (srh at MARY).

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LITERATURE AND HISTORICAL SURVEY

Etymology

The name *Malvastrum* was derived from *Malva,* the generic name for the True Mallows and from the latin substantival suffix "-astrum" which indicates an incomplete resemblance, thus the frequently used common name of False Mallow for members of the genus.

Early treatments of *Malva*

The history of the taxa later transferred to the genus *Malvastrum* is inseparable from that of the genus *Malva* Linnaeus. Linnaeus (1753, p. 687–688) first ordered the members of the genus *Malva* into two informal but coherent assemblages based upon leaf shape, the first being "*Foliis indivisis" with three species and the second termed "*Foliis angulatis" containing the remaining twelve species. This arrangement, adequate for the few species known at the time, was subsequently followed with little change except for the addition of new species by Aiton (1789), Willdenow (1800, 1809), and by R. Brown (in Aiton, 1812).

Cavanilles in his extensive treatment of *Malva* (1786) placed all of the uniovulate species known to him in "Sectio II. Capsulae monospermae", further dividing this section into two subsections

based upon bracteole number: "I. Calyx exterior diphyllus" with six species and "II. Calyx exterior triphyllus" with 37 species. Within subsection II the taxa were placed into two groups according to bracteole shape, the first "A. Laciniae capillares aut angustissimae" with 13 species and a second "B. Laciniae ovatae, aut lanceolatae" with 24 species. Desrousseaux in Lamarck's *Encyclopédie* (1792) chose to follow Cavanilles' arrangement almost exactly, treating 12 "diphyllus" and 42 "triphyllus" species of *Malva* which included several new taxa. The 42 tribracteolate species were placed in two groups corresponding to those of Cavanilles based upon bracteole shape. There were no further innovations introduced beyond his many useful observations on the taxa.

Medicus (1787, p. 37–38) treated 11 species of *Malva* and divded them into two groups based upon the morphology of the mericarps ("Saamen-Kapseln"). The first six species listed by Medicus were said to possess notched and somewhat dehiscent mericarps, and the second five species were said to have stony-layered, indehiscent, and (presumably) unnotched mericarps. It is interesting to note that the first six species (*M. coromandelina* (sic), *M. gangetica, M. peruviana, M. limensis, M. capensis,* and *M. fragrans)* were all later transferred to *Malvastrum* while the latter five species (*M. sylvestris, M. veneta, M. mauritiana, M. verticillata,* and *M. crispa*) remain in the genus *Malva*. No formal status was given to the two groups at this time, however, and the usefulness of this character was largely ignored until again pointed out by Garcke (1857).

Link (1822, p. 209–211) grouped the 39 species of *Malva* known to him into two primary assemblages based upon flower color. His first informal group "A. Cor. flavis" with eight species corresponded in content to the grouping "*Foliis indivisis" used by Linnaeus and his followers, though relying on a different diagnostic character. The second grouping "B. Corollis rubris, albis miniatisve", with 31 species, was further subdivided into "a. Calyce exteriore triphyllo-separato" with 28 species, "b. Calyce exteriore diphyllo" with two species, and "Cal. exteriore triphyllo cum interiore connato" with a single species (*Malva anomala* Link & Otto). The lattermost division was an important innovation for it would later serve as one of the bases for Presl's genera *Anisodontea* and *Malveopsis* (Presl, 1845; Bates, 1969).

The section *Malvastrum* DC.

The epithet *Malvastrum* first appeared in the literature in De Candolle's treatment of the Malvaceae in his *Prodromus* (1824, p. 430) as the first of four sections of *Malva* and contained all of the then known species of *Malva* with the following characteristics: herbaceous or fruticose stems, 2–3-phyllous epicalyx, and monospermous unilocular carpels. The remaining three sections, *Maluchia* DC., *Sphaeroma* DC., and *Modiola* (Moench) DC., differed in one or more respects from these characters. The section *Malvastrum* DC. contained the majority of the 82 species of *Malva* listed by De Candolle, 67 in all, including the well-known European herbs (such as *Malva sylvestris* L., later the lectotype of *Malva* L.) and was subdivided into seven rather well-defined subsections. De Candolle treated all 43 of the taxa contained in Cavanilles' "Sectio II" within *Malva* section *Malvastrum* (with the exception of *M. angustifolia* Cav. which was placed in section III, *Sphaeroma*). Cavanilles' informal subsection I corresponded to De Candolle's formal subsection "3. *Bibracteolatae*" while his more inclusive subsection II was regrouped into the remaining six subsections proposed by De Candolle within the section *Malvastrum*.

The first subsection of the section *Malvastrum, Chrysanthae* DC., roughly corresponded to both the Linnaean grouping "*Foliis indivisis" and Link's grouping "A. Cor. flavis" as mentioned above, its diagnostic characters being a combination of undivided leaves and yellow axillary or spicate flowers. It was this subsection as well as the subsection *Capenses* DC. that contained species later treated as members of the genus *Malvastrum* A. Gray. It should be noted here that, in addition, De Candolle included within *Sida* Linnaeus section *Malvinda* (Medicus) DC. and in the "Species non satis notae" of *Sida* several taxa that would also be included within the genus *Malvastrum* at a later date.

The genus *Malvastrum* A. Gray

In 1849, the American botanist Asa Gray published the new generic name *Malvastrum* in a footnote on page 21 of his paper "Plantae Fendlerianae" with the comment (p. 15) that the name itself was borrowed from De Candolle's section bearing the same name. There has been some debate as to whether or not it was the intention of Gray to elevate De Candolle's section to generic rank

(Fryxell & Hill, 1977; Bates, 1978). It would seem, however, that this was not the case, as evidenced by Gray's own statement (p. 15) that the name was "no longer required now that the corresponding divisions are admitted genera". Gray actually proposed a new genus for which he used the De Candolle sectional name. Gray's stated purpose in proposing the new genus was to leave *Malva* and *Sida* more "natural" and clearly defined. Unfortunately, Gray stated that his "set of ambiguous, perhaps all American, species" were distinguished from *Malva* only by their capitate stigmas, and from *Sida* by their ascending ovule and inferior radicle, useful diagnostic characters, but ones shared by a great number of species that were certainly not congeneric. A summary of the characters used by Gray to circumscribe *Malvastrum* follows: American herbs, flowers axillary or in racemes, calyx with one to three caducous or three persistent bracteoles or these lacking, corolla reddish, orange-yellow, or golden-yellow, stamen tube simple, stigmas terminal and capitate, ovules peritropous-ascending, embryo semi-circular and with an inferior radicle, and carpels muticous or rostrate. Gray expressed particular confidence that his first informal section "Flores miniati" was a natural and essentially the typical one. He also indicated that numerous Andean species for which he did not propose new combinations belonged here. In the second section "Flores flavi" were enumerated only the North American species known to Gray. In fact, his comments on the South American yellow-flowered species indicated his uncertainty as to their proper disposition. His statement that more species were to be included as well as the rather poor circumscription of the genus later led to a large number of new combinations proposed by Gray and others resulting in a taxonomic miscellany of mostly unrelated plants.

The changing concept of *Malvastrum*

Clarification and a strict definition of *Malvastrum* was a gradual development. Walpers (1851) was the first European botanist to accept and treat the new genus and to adhere to Gray's two groupings based upon flower color, involucel-composition, and mericarp characteristics, but only hesitantly transferred two more species into it. Gray himself greatly expanded the concept of *Malvastrum* in 1854 while treating specimens collected in South America by the United States Exploring Expedition. At this time he

made fourteen new combinations and described seven new species, including within the genus the annual blue-flowered malvas (now *Urocarpidium* Ulbrich and *Tarasa* Philippi), the acaulescent malvas (now *Acaulimalva* Krapovickas), and the phyllanthophorous malvas (now *Nototriche* Turczaninow). The latter group of species was placed in a formal new section of the genus, the section *Phyllanthophora* A. Gray ("*Malvastra phyllanthophora*"). This inclusive treatment allowed a more critical review of the infrequently collected and often overlooked South American taxa and clearly indicated that the yellow-flowered South American species were indeed to be considered members of *Malvastrum*. Nevertheless, it weakened the coherence of an already heterogeneous group.

In 1857, Garcke presented a detailed consideration of *Malvastrum* and *Malva* and reviewed the literature, treating every species with which he was familiar. This treatment was particularly important since there was the question among European botanists of the period as to the validity of *Malvastrum*, especially since it was delineated from *Malva* only by its capitate stigmas. Garcke also reviewed the validity of Presl's genera *Malveopsis* and *Anisodontea,* which were also said to have capitate stigmas, and concluded that they were the same entity, yet not necessarily the same as *Malvastrum*. Garcke also noted that *Malvastrum coccineum* more nearly resembled members of the genus *Sphaeroma* (DC.) Schlectendal with respect to its mericarps and so should not be included in *Malvastrum*. Garcke's discussion continued with a review of treatments of *Malva* by De Candolle and by others, indicating which species belonged in *Malvastrum* but in most cases not making the proper combinations. His greatest contributions in this paper were his discussions of specimens now lost, his completeness in indicating synonyms, and his acceptance of Gray's intent in proposing *Malvastrum*.

The species of *Malva* growing at the Cape of Good Hope, treated by De Candolle as *Malva* L. section *Malvastrum* DC. subsection *Capenses* DC., were transferred with additions into *Malvastrum* by Gray and Harvey in Harvey and Sonder (1860). At that time, 18 species were accepted. This group of plants, which included Presl's concepts of *Malveopsis* and *Anisodontea,* has been fully discussed by Bates (1969) in his revision of *Anisdontea* Presl, in which work they were transferred to that genus. The inclusion in 1860 of these

South African species in *Malvastrum* continued to make it unwieldy and contributed towards its reputation as a repository for diverse elements.

The next significant change in the concept of *Malvastrum* appeared in Weddell's *Chloris Andina* (1861). In Weddell's Conspectus (p. 273) *Malva* was characterized by a usually bibracteolate or tribracteolate involucel with peduncles that were axillary or basally attached to the stem, while *Malvastrum* was said to possess exinvolucellate flowers with its peduncles more or less adnate to the petioles. Therefore, Weddell considered *Malvastrum* to be equivalent to Gray's section *Phyllanthophora* alone (all of the 17 species listed are now included in *Nototriche* Turczaninow). Among Weddell's eleven species of *Malva*, eight had been removed from *Malvastrum*, to which they had been transferred in 1854 by Gray. *Malva* as treated by Weddell contained species now referred to as *Tarasa, Urocarpidium,* and *Acaulimalva*. Neither a true *Malva* nor a true *Malvastrum* was included among the 28 species treated by Weddell.

In 1887, while preparing a Flora of North America, Gray again presented a discussion of *Malvastrum* in an attempt to distinguish it more clearly from *Sphaeralcea* A. St.-Hil. He concluded (p. 287 288) "to retain in *Malvastrum* the species with cell of the carpels conformed to the solitary ovule and seed, therefore with no empty terminal portion; and to refer to *Sphaeralcea* those with solitary or occasionally two ovules, which, when the upper ovule is either abortive or wanting, have the upper part, usually the whole upper half, of the mature carpel empty, and of a different texture from the lower [reticulate] part . . .". A treatment of the North American species of *Malvastrum* followed as a footnote to this discussion, and was later presented again and with additions and formal sectional names by Robinson (in Gray, 1897). For the first time, two annual species with elongated peduncles and rose petals, *M. rotundifolium* and *M. exile,* appeared grouped together as the section *Pedunculosa* Gray. The second group of six species in the 1897 treatment with short peduncles and yellow petals, the section *Sidoides* Gray, consisted of what are now treated as the true Malvastrums, while the third and last group of twelve species with short peduncles and scarlet, copper-color, or rose-color petals, the section *Sphaeralceoides* Gray, contained, as currently understood, members of both

the genus *Sphaeralcea* and the genus *Malacothamnus*. *Malvastrum leptophyllum* and *M. coccineum* were retained in *Malvastrum* in spite of Gray's own clarification of *Sphaeralcea,* perhaps because of a previous statement (Gray, 1849, p. 25) that *M. coccineum* was "one of the typical species".

Malvastrum received one of its most complete and important treatments in E. G. Baker's synopsis of the genera and species of the tribe Malveae (1890, 1891, 1894). In this summary a critical examination of all of the names and species then known in the tribe was undertaken, allowing for the first time since Garcke's 1857 paper an extensive appraisal of the species of *Malva* that actually belonged within Gray's concept of *Malvastrum*. In Baker's treatment, (1891, p. 164) *Malvastrum* was again a very inclusive genus characterized by: one to three distinct bracteoles or these absent, stigmas capitellate or clavate, carpels conforming to the seeds, without an empty apical portion. With the last character, Baker clearly followed Gray's final treatment in excluding *Sphaeralcea. Malvastrum* was treated in two groups, not given formal rank, the first of which, the "Capensia", corresponded to those species mentioned above that were treated by Gray and Harvey in 1860, and are now included within the South African genus *Anisodontea* Presl (Bates, 1969). The second, the "Americana", contained 79 species and nine varieties along with their synonymy. Only eight of these names are still in *Malvastrum,* the others having been distributed primarily among ten other genera (*Acaulimalva, Eremalche* Greene, *Kearnemalvastrum* Bates, *Malacothamnus* Greene, *Modiolastrum* Schumann, *Monteiroa* Krapovickas, *Nototriche, Sphaeralcea, Tarasa,* and *Urocarpidium*) discussed in this literature review. As in Gray's 1887 treatment, the true Malvastrums were placed in a single group characterized by yellow petals and a peduncle that was short or absent. Although exceedingly useful as a synopsis, Baker's treatment did not contribute toward a more natural circumscription of the genus.

In the same year that the major portion of Baker's synopsis appeared, 1891, Kuntze resurrected the generic name *Malveopsis* Presl (1845) and treated it as an earlier name for *Malvastrum,* transferring 56 names from *Malvastrum* into that genus. In 1898 he transferred four more names into *Malveopsis* and described two new species. Kuntze's work disturbed several contemporary botanists such as Baker and Schumann (1890, 1891) who had recently

exerted great effort to bring taxonomic order and stability to the group. Rules concerning conservation and rejection of names were demanded at the international level, and as early as 1892 Ascherson published the first list of generic names proposed for conservation, in which *Malvastrum* A. Gray was proposed for conservation against *Malveopsis* Presl. This proposal was undoubtedly submitted by Schumann, who was on the commission responsible for the list. The proposal was acted upon favorably by the International Botanical Congress at Vienna in 1905 (Wettstein et al., 1906) and was included in all subsequent editions of the Code. However, as Bates has pointed out (1969, p. 231), since the name *Malveopsis* applied to a South African genus not congeneric with *Malvastrum,* the proposal for conservation need never have been advanced.

Generic segregates

The process of removing related species-groups from *Malvastrum* as coherent genera, begun to a limited extent by Gray in treating *Sphaeralcea,* soon gained impetus after the synopses of Baker (1890, 1891, 1894) and Robinson (in Gray, 1897) appeared. Greene (1906, p. 208) segregated two groups of species from *Malvastrum* as the new genera *Eremalche* and *Malacothamnus.*

Eremalche Greene consisted of two desert annual species of the Southwestern United States treated as the section *Pedunculosa* A. Gray by Robinson (*Malvastrum rotundifolium* and *M. exile*) and also included the more recently described *M. parryi* Greene. This is a coherent group of species but its generic status was not accepted for many years. In 1936 Jepson referred the species to *Sphaeralcea* (for reasons to be detailed below), and Kearney (1951b) treated the genus as *Malvastrum* section *Eremalche* (Greene) Kearney. However, its generic integrity was accepted by Abrams (1951) and subsequently by Kearney (1955, 1956), as the significance of chromosomal evidence was realized (for *Eremalche, n* = 10, 20) and as other generic segregates were defined.

The proposed segregate genus *Malacothamnus* Greene (1906) consisting of the shrubby Californian species did not gain acceptance for many years. Prior to 1906, the eleven species were distinguished from the other Malvastrums by their shrubby habit, their canescent or tomentose foliage (thus the name meaning "soft-shrub"), and their suborbicular, thin-walled, and completely dehiscent two-valved mature carpels, but the group was not given any

formal status (Robinson in Gray, 1897). Greene's useful but brief treatment was not widely circulated and did not gain acceptance at first as a result of Gray's and Robinson's pervasive influence, except that Abrams (1910) at least temporarily accepted the genus without comment. The first exhaustive treatment of the shrubby Californian Malvastrums by Estes (1925) did not accept *Malacothamnus*, nor did the later more comprehensive treatments by Eastwood (1936) and McMinn (1939). Jepson (1936) transferred all of the species to *Sphaeralcea* (for reasons detailed below). Kearney (1951a), while preparing his review of the American Malvaceae, revived Greene's genus, recognized 21 species and six varieties, and designated *Malva fasciculata* Nuttall as the lectotype species. A haploid chromosome number of $n = 17$ was established for the genus (Webber, 1936). Kearney's treatment stands essentially unchanged today. An unpublished treatment was prepared by Bates (1963), who accumulated data that led him to conclude that several species within *Malacothamnus* should be given subspecific status.

Another important treatment that also helped to clarify the circumscription of *Malvastrum* was that of A. W. Hill (1906, 1909b) who resurrected, amended, and revised the nearly forgotten genus *Nototriche* Turczaninow (1863). Hill's intent was to raise Gray's section *Phyllanthophora*, containing the exinvolucellate Andean species of *Malvastrum* with pedicels and petioles adnate, to generic status. The generic name *Nototriche* Turcz. was available, having been applied to several members of this group previously described as species of *Malvastrum*. About 35 names previously under *Malvastrum* were thereby removed.

In addition, Hill (1909a, p. 218) treated the involucellate acaulescent Andean species of *Malvastrum* as the new section *Acaules* A. W. Hill. The name "acaules" may have been borrowed from Weddell's (1861) informal group within *Malva* under that name, also utilized by Triana and Planchon (1862). The section *Acaules* A. W. Hill was later the basis for the new genus *Acaulimalva* described by Krapovickas (1974a), a genus presently considered to contain 19 Andean species distinguished from *Malvastrum* not only by a series of morphological characters, but also by its different base chromosome number, $x = 5$.

As part of a series of studies on the Rocky Mountain flora, Rydberg (1913) again raised the problem of the status of *Sphaeralcea*. His decision was to merge *Malvastrum* within *Sphaeralcea*

since he felt that the type of the genus must be "the first given binomial under *Malvastrum,* which is *M. coccineum"* (p. 57). His interpretation of *M. coccineum* as a *Sphaeralcea* was correct, but his arbitrary selection of Gray's first species was inappropriate and also violated Article 8 of the Code (Stafleu et al., 1972) in not following Schumann's original choice of lectotype (1890, p. 41). The choice of *M. coccineum* as the lectotype would also necessitate a new name for the yellow-flowered species presently treated as *Malvastrum.* Although Rydberg's lectotype was unofficially published in several editions of the Code in its appended list of conserved genera, the choice was never formally adopted. Instead, Schumann's choice of *Malvastrum wrightii* A. Gray as lectotype has now been formally accepted by the Committee for Spermatophyta (Taxon **27:** 545, 1978). Nevertheless, Rydberg's proposal encouraged numerous transfers of *Malvastrum* species into *Sphaeralcea* (Arthur, 1921, Jepson, 1925, 1936; Metz, 1934). Kearney (1935) clarified the true Sphaeralceas and included still another discussion on the relationships of *Sphaeralcea* and *Malvastrum.* He pointed out for the first time in a footnote (p. 5) and in the text (p. 16) that the Sphaeralceas differed from *Malvastrum* in their basic chromosome number of $x = 5$, a fact later elaborated on by Webber (1936).

Krapovickas (1945), while studying the South American Malvaceae, reviewed the small genus *Modiolastrum,* proposed by Schumann (in Martius, 1891, p. 276). This genus, clearly distinguished from *Malvastrum* by its procumbent habit, its palmately-parted leaves, usually rose-colored flowers, and by the transversely two-chambered mericarps, nevertheless had two names residing in *Malvastrum,* which were removed. Furthermore, Krapovickas (1951) segregated three more species rom *Malvastrum* into a new genus, *Monteiroa,* and included two additional new species. He based the separation on the ventrally and apically dehiscent mericarps, the cymose inflorescences, and a different base chromosome number, $x = 10$. In addition, the chromosomes were seen to be much larger than those of *Malvastrum,* and the flowers were shades of rose rather than yellow.

Continuing his studies of *Malvastrum* and related genera, Krapovickas revised the major portions of the genera *Tarasa* Philippi and *Urocarpidium* Ulbrich. These genera had been accepted since their first publication as being allied to *Malvastrum,* but neither had been comprehensively surveyed until this time. *Tarasa* was distinguished

from *Malvastrum* by its auriculate lilac or blue petals, mostly cymose inflorescences, dehiscent mericarps bearing two apical plumose or pilose cusps, and by its basic chromosome number $x = 5$ (Krapovickas, 1954a). Krapovickas accepted 24 species in *Tarasa,* shifting 20 names from *Malvastrum* to 14 of the species of *Tarasa.* In his study of the genus *Urocarpidium* Ulbrich, Krapovickas (1954b) described the new section *Anurum* containing ten species, a section equivalent to *Malvastrum* section *Peruvianae* Kearney (1951b). In doing so, he distinguished *Urocarpidium* from *Malvastrum* by its irregularly rugose mericarps, its cymose (concinnate) inflorescences, annual herbaceous habit, often lobed leaves, lilac to rose flowers, and by its chromosome number of $n = 10, 15$. In this treatment 11 more names were transferred from *Malvastrum* into seven of the species of *Urocarpidium.*

Malvastrum was redefined by Kearney in 1955 (p. 239), taking into account the new information. His definition follows: "the genus comprises only perennial, often somewhat woody species of tropical and subtropical America having a persistent, triphyllous involucel, yellow corollas, and nearly indehiscent dorsally smooth, laterally smooth or rugose carpels." The chromosomal integrity, $n = 6, 12, 18$, was also indicated and 12 species were enumerated, nine of which are presently maintained exactly as cited.

A particularly useful treament of the five Argentinian species of *Malvastrum* section *Malvastrum* as circumscribed by Kearney was presented by Krapovickas (1975b). In addition a list of 38 excluded species was appended, which was the model for Appendix III in the present work.

Ten years later, Bates added two important studies to the still changing genus *Malvastrum.* In segregating the genus *Kearnemalvastrum,* Bates (1967c) removed two species and seven names from *Malvastrum,* noting that Kearney's revised circumscription could no longer encompass these entities. *Kearnemalvastrum* became a small but coherent genus characterized by white flowers, by black glabrous (or nearly so) unarmed mericarps, and by a chromosome number $n = 16$. His discussion of the two genera clearly indicated a lack of any close relationship between the two.

In contrast to the general trend to segregate species from *Malvastrum,* Bates (1967a) merged the monotypic *Sidopsis hispida* (Pursh) Rydb. back into it. He provided a reasonable argument for doing so (which is accepted in the present treatment) although by

doing so he somewhat extended the generic limits of *Malvastrum*. A redefinition was again provided, this being the most complete description of the genus to that time (Bates, 1967a, p. 16 17).

Since 1967 the two important treatments concerning *Acaulimalva* Krapovickas (1974a) and *Anisodontea* (Bates, 1969) referred to above have appeared. The publication of these two treatments left the remaining true Malvastrums without a complete treatment. The present monograph is intended to fill this gap.

Table 1 summarizes Appendix III in the number of validly published binomials that have been removed from consideration in *Malvastrum* and transferred to genera listed in the left-hand column. Several minor transfers to genera not discussed above have been added for completeness. The reference in which the majority of transfers or new combinations were made is listed in the right-hand column. Appendix III lists all of the names both included and excluded from *Malvastrum* and their current taxonomic placement.

The historical survey presented above has demonstrated that the concept of *Malvastrum* has changed considerably since Gray's original intention to clarify *Sida* and *Malva*. The conception of the genus has changed from a repository for nearly every involucellate

Table 1. **Nomenclatural changes in *Malvastrum***

Genus	Binomials removed from Malvastrum	Primary Reference
Acaulimalva Krap.	23	Krapovickas. 1974a
Anisodontea Presl	26	Bates, 1969
Eremalche Greene	4	Greene, 1906
Kearnemalvastrum Bates	7	Bates, 1967c
Lecanophora Speg.	1	Spegazzini, 1926
Malacothamnus Greene	33	Kearney, 1951a
Malvella Jaub. & Spach	1	Krapovickas, 1970
Melochia L.	1	Krapovickas, pers. com.
Modiolastrum K. Schum.	7	Krapovickas, 1945
Monteiroa Krap.	4	Krapovickas, 1951
Nototriche Turcz.	33	Hill, 1909b
Palaua Cav.	1	Kearney, 1952
Phymosia Desv. ex Ham.	1	Kearney, 1949
Sida L.	2	Gray, 1862
Sphaeralcea St.-Hil.	24	Kearney, 1935
Tarasa Phil.	24	Krapovickas, 1954a
Urocarpidium Ulbr.	10	Krapovickas, 1954b
Total	202	

uniovulate mallow with capitate stigmas, to its present status as a small, clearly delimited, mostly American genus of only 14 species.

DISTRIBUTION AND HABITAT

Contemporary distribution

Members of the genus *Malvastrum* are found primarily in the New World in tropical, subtropical, and warm temperate latitudes between 35°N and 35°S (Fig. 1). The single exception is *M. hispidum,* found between 41°N and 34°N latitudes in the central United States. With the exception of *M. hispidum,* the species are restricted to regions lacking a prolonged period (over three months) of temperature below 0°C and, in fact, most of the species are sensitive to even a brief exposure to this temperature.

Although usually encountered at 0–500 meters elevation at the northern and southern extremes of its range, *Malvastrum* may be found at increasing altitudes of up to 2600 2700 meters towards the equator. *Malvastrum interruptum* and *M. spiciflorum* reach the uppermost altitude limits for the genus. Several species are restricted to the slopes of Central and South American highlands or ranges of moderate elevation (500 2500 m), namely *M. bicuspidatum* (in part), *M. guatemalense, M. scoparioides,* and *M. tomentosum* subsp. *pautense.* The three species that have been introduced into tropical and subtropical regions of the Old World, *M. americanum, M. corchorifolium,* and *M. coromandelianum,* are most frequently found in coastal regions at low elevations. Subsequent expansion in lands with extensive human or animal disturbance (such as India) has been extensive.

A species considered to be both indigenous in and endemic to the Old World, *Malvastrum chillagoense,* occurs in a small area of limestone outcrops at an altitude of 300 400 meters in northern Queensland, Australia. This disjunct distribution remains an enigmatic phytogeographical feature of the genus, along with the distributions of *M. hispidum, M. aurantiacum, M. americanum* var. *stellatum,* and some Australian populations of *M. americanum* var. *americanum.*

One of the greatest concentrations of *Malvastrum* species occurs in a region consisting of northern and northwestern Argentina, southeastern Bolivia, and Paraguay, where half (seven) of the species are to be found. A second area of concentration of species is

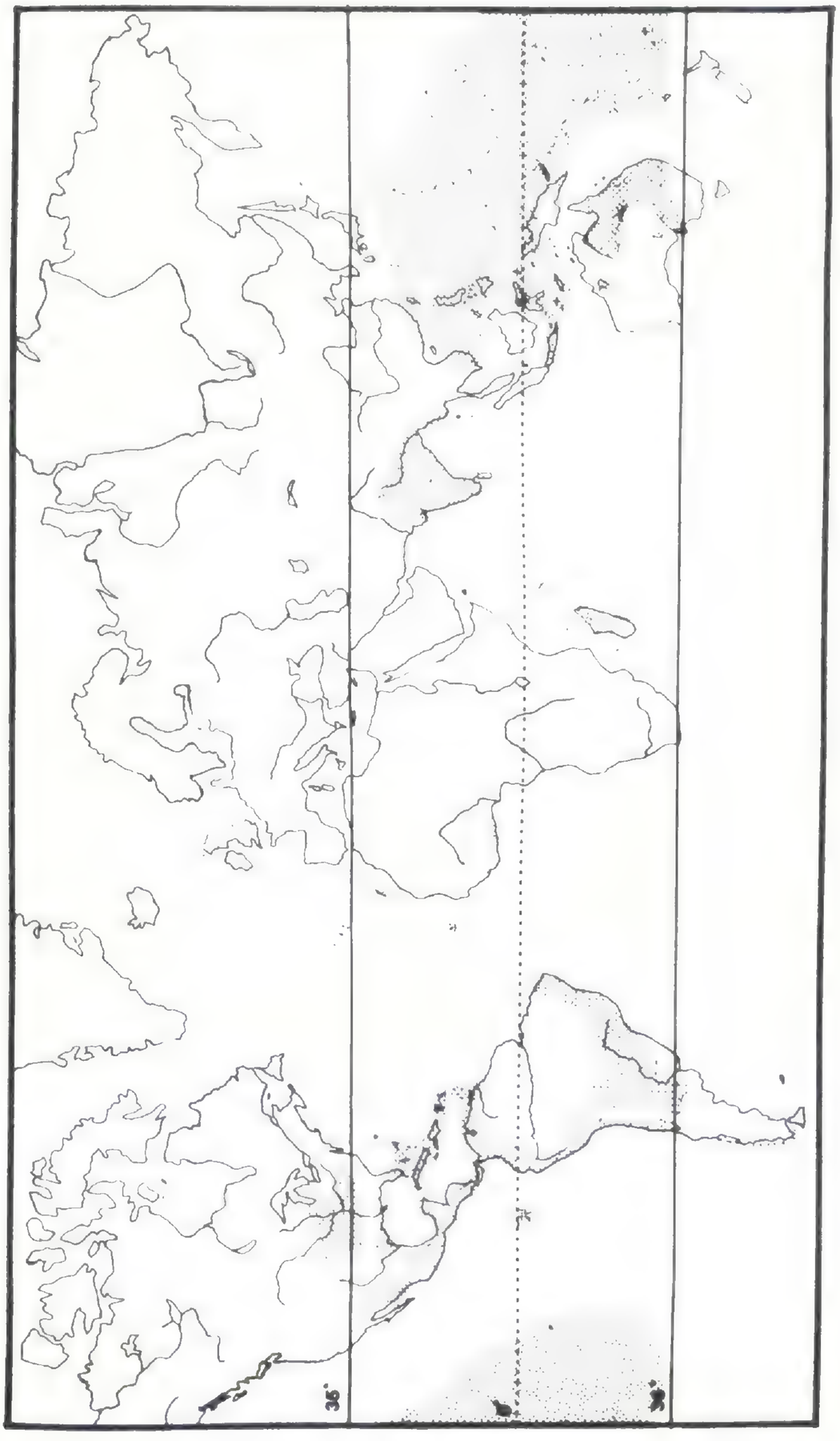


Figure 1. Distribution of *Malvastrum*.

in a larger region extending from northwestern and coastal Peru and coastal Ecuador northward into central Mexico where, again, seven of the species occur. Of the 14 species, all but five (*M. americanum, M. bicuspidatum, M. corchorifolium, M. coromandelianum,* and *M. tomentosum*) have rather restricted ranges, but only three (*M. chillagoense, M. grandiflorum, M. guatemalense*) are here considered to be narrowly distributed endemics. A summary of the taxa and the political regions in which they occur is presented as Appendix I.

Habitat

Although data are not available on every taxon, several species occur in calcareous or alkaline soils varying in texture from loose rock or gravel to fine clay. Populations of the most obvious calciphiles (*Malvastrum chillagoense, M. corchorifolium,* and *M. hispidum*) are best developed and usually restricted to the immediate vicinity of limestone outcrops and their associated thin rocky soils. The preference shown by *M. corchorifolium* for disturbed calcareous gravels and clays is seen in its frequency on the coastal limestones of southern Florida, the Caribbean islands, and the Yucatan. Bates (1967a) has noted in his study of *M. hispidum* that its populations were frequently restricted to a few square meters in the vicinity of limestone outcrops. Herbarium notes for *M. chillagoense,* and to a lesser extent *M. tomentosum* (in Paraguay and southwestern Brazil), also indicate a restriction to limestone outcrops. My own observations on the three species occurring in Texas (*M. americanum, M. aurantiacum,* and *M. coromandelianum*) indicate that the largest populations appear on the alkaline clays and loams of river bottoms and in the agricultural lands bordering those sites, as well as on the calcareous (caliche) soils of low hills, clay pits, road fill, and residential sites.

Other species in the genus do not seem to have such an obvious preference for limestone and may occur in volcanic or granitic soils. This seems to be particularly true of *M. bicuspidatum, M. guatemalense,* and *M. tomentosum* (in Ecuador and Peru), which are not infrequently found in the unstable volcanic zones of Central and South America. A knowledge of the pH requirements of each species, beyond the scope of this study, might further aid in understanding the more subtle points of their distribution patterns.

The adaptation of *M. americanum* and *M. coromandelianum* to the disturbed soils of lowlands and river valleys has apparently allowed them to invade successfully and colonize areas of human environmental disturbance, resulting ultimately in their present wide distributions.

Water requirements and tolerances vary considerably among the species. *Malvastrum aurantiacum* represents one extreme, as it most frequently occurs in wet clay or in periodically marshy areas in full sun along rivers and streams. These poorly drained and often slightly saline flats, while occasionally flooded, are usually dry in the summer to a parched, rock-hard condition. *Malvastrum aurantiacum* is able to survive the periodic semi-aridity by storing water as mucilaginous sap in its elongated and somewhat enlarged taproot and becomes dormant at that season. *Malvastrum americanum* also grows well in an abundance of moisture and may be found in rainforest clearings, slopes, dooryards, and roadsides in areas of heavy rainfall but, in contrast to *M. aurantiacum,* it requires a well-drained soil. *Malvastrum corchorifolium* and *M. hispidum* are quite sensitive to an over-abundance of water. In greenhouse culture these two species are easily attacked by fungi and will not flower when given the same amount of water as *M. americanum* but will produce flowers when the water amount is reduced and the soil is allowed to dry. The remaining species cultured all show their best growth when moderate amounts of water and well-drained soils are provided.

Hypothetical geographical origin and dispersal

The interpretation of the origin and subsequent dispersal of *Malvastrum* is not aided by the fossil record. Even today, none of the species are frequent in areas of sedimentation. On the contrary, many are found on mesic to semi-xeric slopes or outcrops, or in disturbed land where preservation is highly unlikely. A leaf impression discovered in Oligocene ash deposits at Florissant, Colorado, was named *Malvastrum exhumatum* by Cockerell (1906), but an examination of the photograph and description indicates that this is the leaf fragment of a *Sphaeralcea* (see Appendix III).

In reconstructing the geographical history of the genus, I have considered: 1) the present distribution of clearly indigenous or endemic species; 2) the geologic history of the region thought to be its area of origin; 3) the relative number of specialized and

unspecialized characters shown by taxa; and 4) examples of other genera with similar distributions, ecology, and dispersal mechanisms.

Of the 14 accepted species, six are endemic to South America and two more have their greatest frequency and diversity there (*Malvastrum americanum, M. coromandelianum*). Of the remaining six not found in South America, one is of probable hybrid origin (*M. corchorifolium*), two are clearly derived from South American members of the section *Tomentosum* (*M. cuspidatum, M. guatemalense*), and three (*M. aurantiacum, M. chillagoense, M. hispidum*) will be treated individually as phytogeographic problems. With respect to the primary generic distribution pattern, however, a proposal indicating South America as the ancestral home for *Malvastrum* seems reasonable.

Among the major geologically stable regions known in South America are three pre-Cambrian shields (Guyana shield, Central Brazilian shield, East Brazilian shield) and several massifs (Pampean Ranges, Patagonian, Deseado) (Haffer, 1974). *Malvastrum* is most diverse on the Pampean Ranges massif, the region consisting of the subtropical and warm temperate chaco and Paraná basin as well as the comparatively low eastern foothill ranges of northwestern Argentina and Bolivia. This diversity of habitats supports the greatest number of species (seven) in the smallest area for the genus as a whole. Based upon this contemporary distribution and known geologic changes in South America, one can be confident that the genus has had a long history in that region. It is not a component of the Guyana shield nor Amazonian basin floras but, instead, it is a component of the highland arc that is nearly continuous in either direction from the pampean ranges around the Amazon basin (Fig. 1).

If one follows the assumption that the present center of diversity for a genus indicates not only its long history but also its center of origin (Willis, 1922, 1949) then this Pampean region would be that area for *Malvastrum*. However, such a diversity center may also simply reflect the geologic stability of this region as compared to the instability of other areas of South America, thus allowing the persistence of the species. This would be the 'museum hypothesis' of Stebbins (1974, p. 166). The third hypothesis would be that the area of greatest diversity indicates a region of secondary speciation. For

this last hypothesis to be reasonable, one must demonstrate that all of the species involved are closely related.

One can examine the charactertistics of the taxa inhabiting the possible area of origin to evaluate the hypotheses. The process of secondary radiation or speciation does seem to explain subspeciation in *M. bicuspidatum* in Central America, but this same subspeciation cannot be demonstrated in the pampean region. Instead, in this region are found several of the most distinctive and divergent species of the genus. One of these, *M. spiciflorum*, is the only diploid extant ($n = 6$) and has scarcely modified mericarps, autogamous flowers, and other unique features (cf. Appendix II). This diploid shares its range with the tetraploid *M. grandiflorum* ($n = 12$) which has elaborately ridged, winged, and cuspidate mericarps, and entomophilous flowers that are self-sterile. Also present and overlapping in range is the hexaploid *M. interruptum* ($n = 18$). Furthermore, *M. coromandelianum* and *M. americanum* have les weedy and somewhat restricted morphotypes here (some given formal rank) that do not occur where the more widespread pantropical forms live, suggesting a long history for those species in this region.

To understand better the history of *Malvastrum* in the context of geologic change it is important to present a brief overview of these events in South America (Haffer, 1974; Vuilleumier, 1971).

Proponents of plate tectonics have supplied data indicating that until the late Cretaceous portions of northeastern South America and western Africa remained in close proximity while the southern portions of the two continents had separated much earlier. While the new continent sloped gently westward into the Andean geosyncline upon separation from Africa, there was a subsequent pronounced emergence of the Brazilian shields and a gentle subsidence of the middle Amazon basin during the late Cretaceous that continued into the Tertiary. The lack of indigenous Malvastrums or even close relatives in western Africa or on the ancient Guyana and Brazilian shields suggests that the genus appeared in more recent times.

According to McLean and Ivemey-Cook (1967), during the Eocene the flora of latitude 38° S in central Argentina (in the vicinity of the present *Malvastrum* diversity center) was fully tropical, while 4° farther south at latitude 42° S the surface was probably covered

by a subtropical woodland with surrounding pampas, a vegetation type more suitable for the genus. Cooling occurred during the Oligocene, and by the Miocene temperate elements of the Antarctic-Tertiary flora replaced the tropical floras of southern Chile and Argentina, indicating northward migration. The climate in northwestern South America was probably more humid than during the early Tertiary and permitted the existence of luxuriant plant life, as documented by thin coal seams in Miocene deposits there. This humid flora would have been generally unsuitable for Malvastrums. It would seem, then, that by the Miocene the genus or its ancestors could have been centered in the pampean ranges.

From the mid-Tertiary onward, open savannas, patches of rain forest, and vast mud flats probably were found in the eastern foothill belt of the present Andes, while the upper part of the Amazon valley was filled by a large inland sea. The central and southern Andes were still low-lying islands and permitted the strong drying influence of the Humboldt Current to reach far inland to the east. This correlated with an expanse of semi-xeric vegetation for which such taxa as *Malvastrum tomentosum* would have been well-suited.

In the late Pliocene a continuous land-bridge was finally formed as the Central American system became continuous with the Andean system. Not until the continuous land connection formed did major faunal and floral exchange of northern and southern forms take place. Since the Andes were much lower at that time, and since dense forests were by then limited by the aridity of the epoch, various north-south invasion routes allowed migration through northwestern Colombia, more than at any other period prior to the final uplift of the Andes and prior to the expansion of the tropical lowland forests. Since most Malvastrums have fur-attachment mechanisms, this would have been the most significant period in its dispersal.

The events of the Pleistocene epoch brought about present topography and distribution patterns. First, the main uplift of the Andes during the late Pliocene and early Pleistocene led to extensive eastern rains and the expansion of humid forests onto the emerging Amazon basin. Second, the uplift must have forced a rapid adaptation, evolution, or extinction of species inhabiting the elevating Andean belt. Third, the periods of mountain building eventually led to climatic deterioration and temperature decrease during the cold

periods of the Pleistocene (Barghoorn, 1964) that would have forced migration. During the peak phases of glaciation, rainfall decreased and strong arid conditions again prevailed in many regions, restricting humid forests to refugia. During warm phases the humid forests expanded. Damuth and Fairbridge (1970) have traced the westerly air flow against the southern and central Andes that during peak glaciations led to extensive cool deserts east of the mountains.

While glacial climates lowered both the snowline and timberline in the high plateau of southern Peru, western Bolivia, and northwestern Argentina, there is no evidence of radical climatic changes in the eastern pampean foothills that would have decimated the flora. In addition, there were no barriers to migration in that area to warmer regions of the north or east except, perhaps, for the occasionally submerged Paraná basin. Since the last glaciation (ca. 15,000 yrs b.p.) humid forests have again expanded and recolonized the basins, leaving isolated remnants of the formerly widespread semi-arid woodlands and savannas on the highlands and sands surrounding the Amazon.

My hypothesis is, then, that *Malvastrum* first appeared and diversified in the diverse habitats of the pampean massif and the mesic to semi-xeric regions that were apparently continuous in a western coastal band reaching from this region north to Colombia and Venezuela and east to the Brazilian coastal highlands before the Andes orogeny. The submerged Paraná basin may have isolated the genus from the eastern Brazilian shield in its earliest phases. As the Andes arose, *Malvastrum* populations were probably able to persist and migrate along lower elevations until aridity and cold exterminated them. The present discontinuous distribution of *M. tomentosum* (Fig. 37) would appear to be evidence of a greater range during the periodic xeric phases of the Pleistocene or earlier. The formation of the Central American landbridge in the Pliocene resulted in the transport of those species adapted to mammalian transport out of South America and, in at least the section *Tomentosum,* secondary speciation in the new environment. The several species in the Argentinian-Bolivian foothills that were not adapted for animal transport or that could not migrate along xeric lowlands remained in their general area of origin. The result was a southern center of diversity and a northern center of lesser diversity separated by a vast inhospitable Andean and rainforest terrain. The final event in *Malvastrum* dispersal occurred in man's accidental

transport of the clinging seeds to areas of the Old World tropics.

Malvastrum is only one of several genera of the Malvaceae with similar distributions. For example, *Tarasa,* found in northwestern Argentina north and west to Chile, Bolivia, and Peru, has a disjunct distribution in Mexico. Members of that genus have colonized higher elevations in the Andes than *Malvastrum* and this correlates with changes in ploidal level (Krapovickas, 1960). *Sphaeralcea* is a genus with semixerophytic tendencies with its center of distribution in western South America and then again in northern Mexico and western North America. *Urocarpidum* also has a very similar distribution, occurring from northwestern Argentina, Bolivia, and Chile in the south, northwards nearly continuously to Colombia and Venezuela along the Andes and again in Mexico at high elevations. The species, like *Tarasa,* are better adapted to high elevations and cold than *Malvastrum*, occurring up to 3800 m in the southern latitudes and as far south in Chile as 30° S latitude. The distribution of the American species of *Cienfuegosia* is also remarkably similar to that of *Malvastrum* (Fryxell, 1969). Several of its species are found in the Pampean ranges and Chaco region as well as in the Paraná basin. The distribution of *C. argentina* closely matches those of *M. amblyphyllum, M. interruptum,* and *M. spiciflorum;* that of *C. tripartita* matches that of *M. tomentosum* in western South America. In general, the ranges of the two genera coincide except that some species of *Cienfuegosia* are more frequent in the Planalto of south-central Brazil and at least one (*C. affinis*) is present in the Guyana highlands. *Cienfuegosia* seems to be a much older genus than *Malvastrum*, as one subgenus is also indigenous in Africa, its distribution providing some evidence for the former connection and proximity of the two continents. Other genera in other families also show the pattern of distribution shown by *Malvastrum;* some of these distributions are summarized by Rzedowski (1978, Chapter 6) and Raven (1963).

Long distance dispersal

There remain three species in their entirety (*Malvastrum aurantiacum, M. chillagoense,* and *M. hispidum*) and two species in part (certain forms of *M. americanum* var. *americanum* in Australia, *M. americanum* var. *stellatum,* and *M. coromandelianum* in Texas and northern Mexico) that may have been distributed by means of long distance dispersal. Long distance dispersal by birds has often been

proposed for such disjuncts. Sound evidence that this may actually occur has been presented by Cruden (1966) and Proctor (1968). Raven (1963) summarized the known and suspected amphitropical disjuncts and presented several important observations summarized here: 1) the plant communities involved are relatively recent in origin; 2) the amphitropical disjuncts are plants that occur in open or weedy habitats such as seasonally moist places where establishment would be relatively easy; 3) nearly all of the plants are autogamous or self-compatible; and 4) many of the disjunct patterns correspond with the migration routes of birds, which must occasionally carry seeds between one hemisphere and the other.

Most populations of *Malvastrum coromandelianum* subsp. *coromandelianum* in Texas and northern Mexico are morphologically very similar to those of the lowlands of Paraguay and northeastern Argentina, particularly with regard to their ascending stems and the appressed 4-rayed bilateral rather than simple hairs on the upper leaf surfaces. These two disjunct populations in their natural state occupy similar environments, i.e., typically low, periodically wet, loamy or clay areas along river floodplains, from which they may spread to other disturbed areas. Since the Texas and northeastern Mexico populations differ from those of southern Mexico and the Caribbean but yet resemble again those of the South American Paraná basin, I feel that they represent a separate introduction. Applying Raven's principles to *M. coromandelianum* subsp. *coromandelianum* in Texas: 1) the populations occur in the coastal plain and central and southern river systems of Texas and northern Mexico east of the Edwards plateau, an area mostly under water during the late Tertiary and so floristically rather young; 2) the populations occur in disturbed river bottoms and seasonally wet areas; 3) greenhouse observations have shown that the Texas (and all other) populations are autogamous; and 4) the disjunction corresponds with the western branch of the Mississippi flyway. A proposed fifth principle is that the disjuncts often have smaller flowers than those of the source population. An alternative explanation for the occurrence of the Texas population with Paraná basin affinities would be through human introduction. While its range has undoubtedly been expanded in Texas by man's destruction of the environment, the form has been present at least since the earliest days of botanical exploration in the state in the early and mid 1800's (Berlandier and Lindheimer collections) when it occurred in areas

relatively undisturbed by man. In more recent times, the adventive Central American-Pan Caribbean (and Pan-Tropical) form with simple upper leaf hairs has become established particularly near Houston and in other scattered southern Texas localities, and now intergrades freely with the indigenous population.

Malvastrum aurantiacum is found in similar often low lying, wet habitats in Texas, particularly near the coast, often with the indigenous *M. coromandelianum* population. The species is also autogamous but maintains a well-developed outcrossing potential. Unlike *M. coromandelianum*, however, this species is not known to occur in South America, and has no known close relatives. It is a morphologically distinct and specialized hexaploid species ($2n = 36$). Its distribution and habitat correspond to a major extent with that of other disjuncts in the region, such as *Cienfuegosia drummondii* (A. Gray) Lewt. which is found in similar habitats in the Paraná basin in South America. Fryxell (1967) has presented a case for the likelihood of long-distance dispersal in that species. It is my opinion that *M. aurantiacum* also reached Texas in ancient times in this manner and that its ancestors have become extinct in South America since that introduction. Migration seems unlikely since no other populations exist. Its fruits just previous to maturity are rose-red and probably attractive to birds. Evidence for its ancient occurrence in Texas is provided by the presence of an undescribed species of the Anthonomid weevil genus *Macrorhoptus* whose life cycle depends entirely (as far as is known) on this plant (Burke, 1973). Other genera and species found in Texas in the same general region as *M. aurantiacum* that show the same pattern of disjunction, are: *Bothriochloa exaristatus* (Nash) Henr., *Chloris pluriflora* (Fourn.) Clayton, *Cressa nudicaulis* Griseb., *Desmanthus brevipes* B. L. Turner, *Gaillardia* spp., *Hedeoma* spp., *Hymenoxys* spp., *Leptochloa dubia* (HBK) Nees, *Lycium* spp., *Menodora* spp., *Phyla* spp., *Prosopis reptans* Benth., *Salvia* spp., *Sida* spp., and *Xanthocephalum* spp. (Raven, 1963).

The distributions of the remaining 3 disjuncts do not fit the general pattern presented by Raven (1963). *Malvastrum hispidum*, *M. chillagoense*, and *M. americanum* var. *stellatum* seem to belong to old vegetation communities, and do not occur in open, moist, or weedy habitats.

While *Malvastrum hispidum* occurs near the Mississippi bird migration route, *M. chillagoense* seems isolated from such routes.

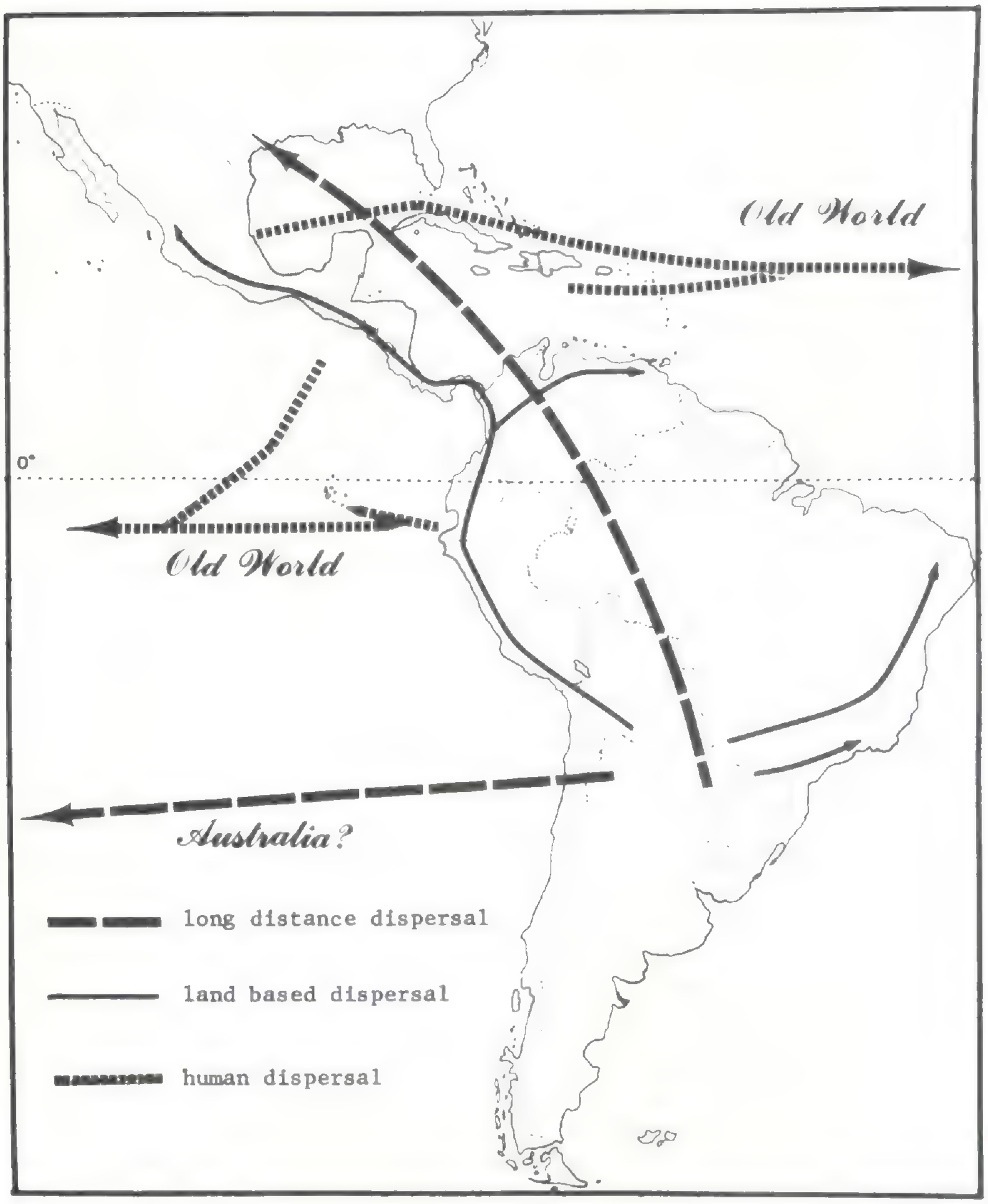


Figure 2. Hypothetical dispersal routes for *Malvastrum*.

However, both seem to be autogamous species, *M. hispidum* not infrequently being also cleistogamous. While each is primitive in some respects, each is specialized in others. *Malvastrum hispidum* is a hexaploid ($n = 18$), and is assumed not to be relictual or particularly ancient within the genus. There are no additional data that might lead to a distributional history for either species. My opinion is that *M. hispidum* is an ancient long-distance disjunct that survived the glacial epochs in the Ozark refuge. *Malvastrum*

chillagoense may also be a long-distance disjunct, although considering the distance involved this seems unlikely. It would be easily explained if eastern Australia and western South America had been joined in the past. An alternative explanation is that it is a more recent derivative form from *M. americanum* (once thought to have been solely introduced to Australia and distributed widely by grazing mammals) since the two species have a significant number of morphological characters in common and nearly identical pollen grains. This presents a problem, namely, has there been sufficient time for its divergence from *M. americanum*? Also, what would explain the retention of several primitive characters, such as the free bracteoles? The fact that it is restricted to limestone is also a unique feature. There are no chromosome counts for this infrequently collected species.

Judging by the great diversity in *Malvastrum americanum* in Australia and its presence in native vegetation types, there is some reason to suspect that this species also has a far longer history on that continent than previously thought. It has been collected in rather inaccessible areas since at least the 1830's. Nevertheless, evidence suggests that at least some Australian populations of *M americanum* could have been recently introduced since: 1) several collection labels indicate that sheep, cattle, and horses are fond of the old dried seed heads, and since sheep are not only a very early introduction but also nearly ubiquitous, a rapid range extension could have resulted from a chance introduction, and 2) the range of variation of most populations fits into the periphery of the range of variation shown by *M. americanum* in the American tropics. Until a chromosome count has been made and it has been studied in greenhouse culture, conclusions as to the origin of *M. chillagoense* and the Australian variants of *M. americanum* remain very speculative.

Figure 2 illustrates the hypothetical dispersal routes discussed in this section. The primary routes include: 1) long-distance dispersal as in *M. aurantiacum, M. coromandelianum* subsp. *coromandelianum* in part, *M. chillagoense,* and *M. americanum* in part; 2) land-based animal dispersal by means of ornamented or cuspidate fruits as in *M. tomentosum* and its allies, *M. coromandelianum* in part, and *M. americanum;* and 3) disperal by man as in the cases of *M. americanum, M. corchorifolium,* and *M. coromandelianum* subsp. *coromandelianum.*

ETHNOBOTANY

While species of *Malvastrum* have never been of great importance to man, several have been companion plants to man in the tropics. As a result, they have been generally recognized, named, and examined for possible uses.

The use of *Malvastrum* species as brooms is well documented. L'Heritier (1786) described *Malva scoparia* (= *Malvastrum tomentosum*) from Peru and stated that the inhabitants of the region made cheap brooms from this bushy plant ("Scopas sat viles e ramis conficiunt incolae", p. 54). The common names attributed to the plant were "balai sauvage" (French) and "escoba cimarrona" (Spanish). In the following year, Jacquin (1787, p. 59) described a different *Malva scoparia* (= *Malvastrum corchorifolium*) from Haiti which he said the inhabitants called "herbe a balay" for the same reason. "Escoba" or "broom" is a general name applied to several unrelated dooryard plants used in this manner, such as *Parthenium, Sida, Melochia,* and *Scoparia,* as well as *Malvastrum.* In addition to the two species named above, *M. americanum* and *M. coromandelianum* are also called "Escoba" or "Escobilla."

Other names, often somewhat descriptive, have also been applied to the weedy species: e.g. *M. americanum,* "Olotillo" ("little corn cob", El Salvador), "Mozote" ("stickseed"), "sheepmallow" (Australia); for *M. coromandelianum,* "Wild Okra" (Bahamas), "wire weed" (Virgin Islands). The general name "Malva" is also encountered in Latin America for the weedy species.

Malvastrum coromandelianum (and probably *M. corchorifolium* in Yucatan) has had medicinal uses. A specimen collected in Coahuila, Mexico (*Gregg 337*) bore the notation that the plant was used for emollient poultices and against headaches. Standley (1930, p. 349) stated that "The plant has emollient properties. Its decoction is employed to cleanse sores and as a remedy for dysentery." In Haiti, *M. corchorifolium* is occasionally used in a similar manner for the stomach (label data, *Leonard 13497*). The only clinical laboratory of which I am aware concerning *Malvastrum's* medicinal value was conducted by Vermeersch et al. (1972). *Malvastrum coromandelianum* infusions were used for their hypotensive properties by the inhabitants of parts of Madagascar. Results indicated a slight hypotensive result, and histological studies of test animals indicated a histaminic effect on the smooth muscle fiber of the blood

vessels and intestines. Although this hypotensive effect is somewhat unusual, the emollient quality due to foliar mucilage is a characteristic of many members of the Malvaceae.

In Australia, *M. americanum* has been thought to cause illness in livestock (*Gessler s.n.* (BRI): "Reported that it is eaten by sheep and causes them to have a hump in the back and lose their ability to walk"; *Grummitt s.n.* (BRI): "Suspected of being responsible for a sickness in sheep"). The animals, nevertheless, are reported to eat the plant eagerly. The poisoning may actually be the result of a high concentration of selenium in the soil (*Murphy s.n.* (BRI): "Voucher for selenium determination. Collected from a known poison strip") since poisoning from this species is not known to occur elsewhere in its range.

PHENOLOGY AND REPRODUCTIVE BIOLOGY

Of the 22 taxa presently recognized in *Malvastrum*, individuals of 16 were grown to maturity in the greenhouse (11 of the 14 species) and their growth characteristics were observed. Three species (*M. americanum*, *M. aurantiacum*, and *M. coromandelianum*) were also studied in naturally occurring populations in Texas. The remaining entities are known from very few collections and were not observed in the living state. The data on phenology and reproductive biology summarized in this section result from these greenhouse and field observations as well as from inferences based upon preserved materials. The features discussed here include: 1) seed longevity and germination, 2) plant-maturation and seasonality, 3) the duration and pattern of anthesis (floral phenology), 4) fruit-maturation, and 5) pollination-mechanisms and vectors.

Seed longevity and germination

Malvastrum seeds are extremely durable. The seed coat is thick (0.1–0.3 mm) and composed primarily of radially elongated, narrow, densely-packed, highly lignified cells (see Fig. 15). Greenhouse plantings have shown that seeds as much as 46 years old can be viable (e.g., seeds from *Steere 1010, M. corchorifolium*, collected in 1932), and germination of seeds 20–40 years old is not infrequent. The seeds can pass through the digestive systems of birds and cattle without damage, as personal observations of the Texas species

attest. I have observed *M. coromandelianum* seedlings in old fecal matter in Texas pastures, and have seen sparrows eating and scattering the seeds of the same species in the greenhouse. The seeds may germinate a few days after being shed from the plant in some species (particularly *M. coromandelianum*) or may undergo a dormancy period and germinate the following spring or during favorable periods of subsequent years (as observed in *M. aurantiacum*). Most seeds examined, except those of *M. coromandelianum*, seemed to require a dormancy period and did not germinate simultaneously, but differentially over as much as a year or more. Seeds of *M. amblyphyllum*, *M. americanum*, *M. corchorifolium*, *M. coromandelianum*, and *M. grandiflorum* generally germinated in 3–5 days after planting. The other species usually required 14–30 days for germination under the same conditions. It seems significant that seeds of the three weedy species germinated rapidly and had particularly long-lived seeds. Members of the section *Tomentosum* as well as *M. aurantiacum* required the longest period before seed germination, from 7 to more frequently 14–30 days. Perhaps this is a result of the unstable environmental conditions where these occur.

Maturation and seasonality

In the greenhouse the taxa, planted simultaneously in March, matured at quite different rates. *Malvastrum coromandelianum* subsp. *coromandelianum* is, compared to the other Malvastrums, a precociously flowering taxon and produces its first flowers after 50–60 days of growth, often at the sixth leaf node above the cotyledons. Several individuals produced flowers when only 7–10 cm tall. This is interpreted as being correlated with its weedy habit, and may reflect a neotenous developmental pathway. *Malvastrum coromandelianum* subsp. *capitato-spicatum* also required 50 60 days of growth before anthesis but first flowered at heights of 20 cm or more. The warm-temperate species *M. aurantiacum* requires 60–65 days before anthesis, followed by *M. hispidum* requiring about 60 days. The southern hemisphere warm-temperate *M. grandiflorum* requires 60–70 days of growth before flowering. Next to attain reproductive capability were *M. americanum* (90 days) and *M. corchorifolium* (90–120 days). The remaining plants required 100–180 days from germination to the first flower, these being *M. bicuspidatum* (all three subspecies grown), *M. scoparioides*, and *M.*

tomentosum (both subspecies). Specific periods required for each taxon for maturation and other processes are included in the individual taxonomic treatments. Several trends were seen: 1) the weedy species were among the first to flower, 2) the temperate species also flowered early, and 3) taxa from semi-xeric and tropical regions were among the last to flower.

Floral phenology

Most of the taxa examined flowered in the greenhouse in the autumn months (September–December) and continued through the early winter if not cold-damaged. *Malvastrum coromandelianum* subsp. *coromandelianum* and subsp. *capitato-spicatum* flowered continuously from spring through to the early winter. The Texas populations of *M. americanum* occasionally flowered in the early summer, but all tropical populations of the species grown in the greenhouse did not flower until the autumn. The Texas *M. auran-tiacum* flowered in the late spring (May, June), became dormant during the driest summer months, flowered again in the early autumn, and became completely dormant by the end of November. The pattern of flowering in the spring and autumn with dormancy in the summer was also shown by *M. grandiflorum* and *M. bicuspi-datum* subsp. *bicuspidatum*. The remaining taxa flowered only in the autumn. Data from herbarium specimens indicate that the seasonal pattern seen in greenhouse plants is more or less typical of patterns in native populations.

Flowers were produced for periods of time varying from one to two months (*M. amblyphyllum, M. bicuspidatum* subsp. *campanu-latum* and subsp. *tumidum, M. grandiflorum, M. scoparioides*) to over 9 months (*M. coromandelianum* subsp. *coromandelianum* and subsp. *capitato-spicatum*). The remaining taxa were intermediate in inflorescence duration and flowered for 3–7 months out of the year. Each flower typically was open for only a few hours on a single day.

Figure 3 presents data on the daily flowering periods that were observed in this study (the times have been adjusted to local standard time). The solid lines indicate the usual duration of open flowers and the dashed lines indicate exceptional flower periods. The following trends were observed: 1) flowers opened at various times of day but more frequently in the late afternoon; 2) taxa with mostly autogamous flowers (*M. amblyphyllum, M. americanum, M. corchorifolium, M. coromandelianum,* and *M. hispidum*) bore

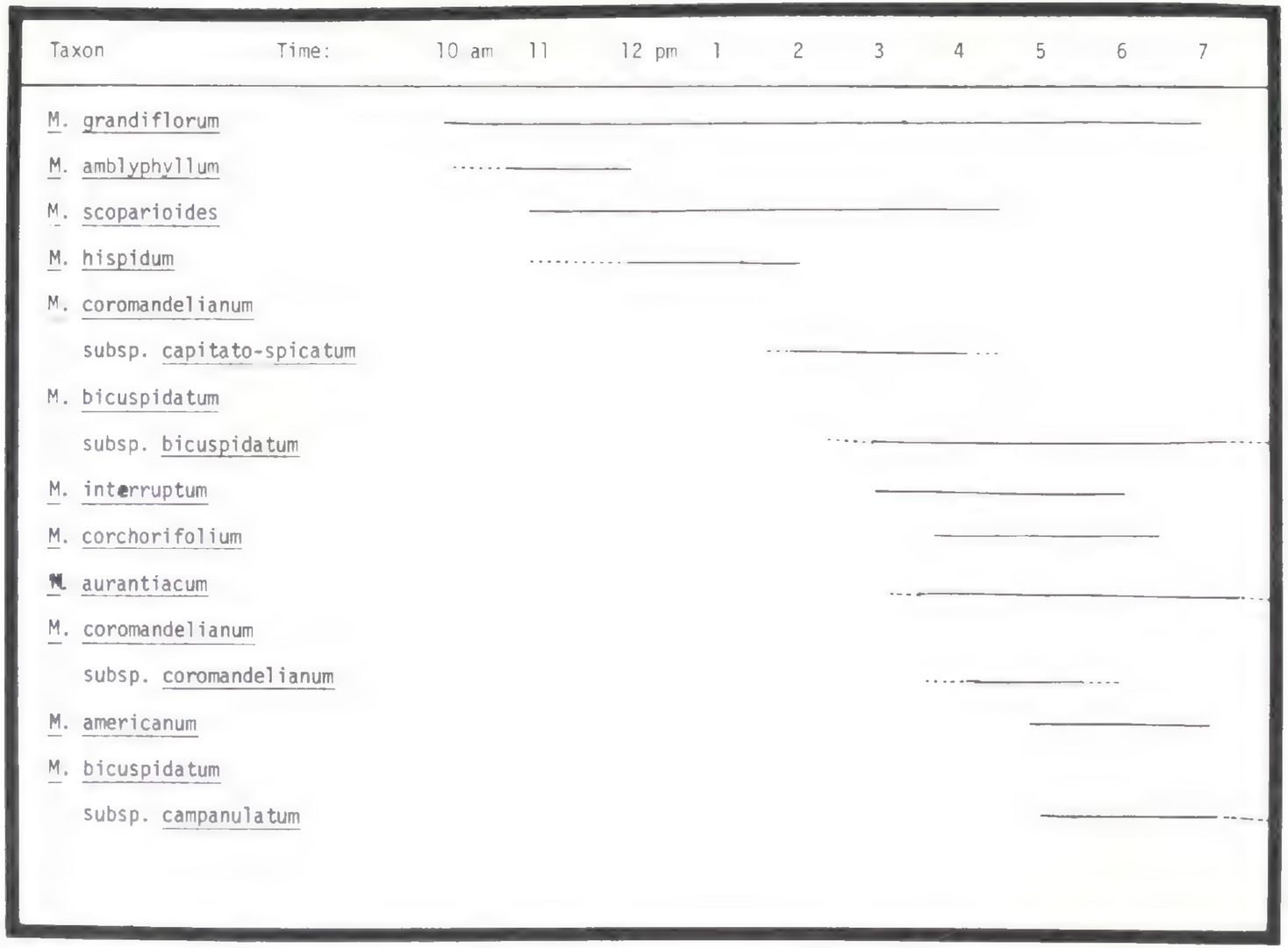


Figure 3. Daily flowering periods in *Malvastrum*. Local standard time.

open flowers for only 1.5–2 hours, while those with outcrossing or potentially outcrossing flowers bore open flowers for 3 9 hours (*M. aurantiacum, M. bicuspidatum, M. grandiflorum, M. interruptum, M. scoparioides*). Infrequently during cooler weather, flowers of several individuals of *M. bicuspidatum* subsp. *bicuspidatum* and subsp. *campanulatum* remained open through the night and most of the next day. This may also be true in the wild populations of those taxa since the latitude at which these were cultivated did not differ greatly from that of the seed sources.

Flowering periodicity has aided taxonomic conclusions. Within *M. coromandelianum*, the individuals referred to subsp. *capitato-spicatum* bore flowers that opened and closed earlier than those of subsp. *coromandelianum* even when the seed sources were from the same geographic area. This would isolate these from crossing where their ranges might overlap, and so has aided in defining the subspecies. A second observation was that the flowers of *M. corchorifolium* closed after those of *M. coromandelianum* subsp. *coromandelianum* and before those of *M. americanum*. This not only suggests the importance of genetic controls on flowering but also gives further support for belief in the hybrid origin of that taxon from the latter two (see Table 4). Support for the close relationship of *M. amblyphyllum* with *M. grandiflorum* (members of the section *Amblyphyllum*) is seen in the late morning or midday anthesis shown by those two taxa. The sequence of flowering remained constant from day to day and was a useful taxonomic character.

V..riation in the flowering schedule occurred only on cool or overcast days and also followed seasonal daylength changes. Several taxa flowered earlier in the day on cool overcast days than on warm sunny days. Wild populations of *M. aurantiacum* infrequently produced open flowers at noon or else failed to blossom in such weather. In those taxa that had long flowering periods, flowers opened and closed as much as 2 hours earlier in the winter months (December–February) than in the summer (June September). Nevertheless, the sequence of flowering among the taxa remained constant, e.g. flowers of *M. coromandelianum* subsp. *capitato-spicatum* were always closed by the time those of subsp. *coroman-delianum* opened.

Fruit maturation

The time required for fruit maturation (anthesis to the dry fruit) was also recorded for several of the taxa. *Malvastrum americanum* and *M. coromandelianum* fruits ripened the most rapidly, in 15–19 days and 17–22 days after pollination, respectively. The speed of fruit maturation is correlated with the weedy habit in both species. Of the remaining taxa observed, ripening occurred as follows, the taxa listed in the order of increased ripening time: *M. interruptum* (21–26 days), *M. bicuspidatum* subsp. *bicuspidatum* (23–29 days), *M. corchorifolium* (24–36 days), *M. amblyphyllum* (29–33 days), *M. bicuspidatum* subsp. *campanulatum* (ca. 30 days), *M. grandiflorum* (30 days) and *M. aurantiacum* (33–34 days). The order of ripening follows directly from the fruit size; smaller fruits matured more rapidly than larger ones. Since the maturation times overlap to such a significant extent in this second group of taxa, the character is not of great diagnostic value.

Pollination mechanism

The flowers of *Malvastrum* are perfect and homogamous, that is, the stigmas and stamens mature at the same time. However, this can be affected by environmental conditions. In *M. interruptum,* a species from temperate high altitudes, the anthers did not dehisce at all during the warmest (29–35° C) late summer days. On the cooler days of autumn, normal anther dehiscence occurred. In those taxa that were primarily autogamous (*M. amblyphyllum, M. bicuspidatum* subsp. *campanulatum, M. chillagoense, M. corchorifolium, M. coromandelianum* subsp. *capitato-spicatum, M. hispidum*) pollen was shed directly onto the stigmas as the petals opened making natural crossing difficult. In contrast the remaining taxa, at least in early flower, had exserted stigmas that prevented early self-pollination and promoted outcrossing. With the exception of *M. grandiflorum* and *M. scoparioides,* the stigmas of members of this group recurved into the anther cluster and self-pollinated, usually as the flower began to wilt. The species were seen to be, for the most part, self-compatible and produced high percentages (80 90%) of viable seed. Exceptions include *M. grandiflorum, M. interruptum, M. scoparioides,* and *M. bicuspidatum* subsp. *tumidum,* all of which produced very low percentages (ca. 10% or less) of viable seed when self-pollinated and which may have incompatibility mechanisms not

yet understood. Since seeds failed to develop on flowers that were emasculated, apomixis does not seem to be involved, nor is it suspected in any taxon.

In *M. hispidum* the extreme condition of cleistogamy can occur and fruits are produced as a result of pollen shed on the stigmas in bud. Apparently the stigmas are recurved into the anther cluster precociously. Seed set is ca. 90% in this species. The reduced number of carpels and stamens in this and other taxa is correlated with autogamy and cleistogamy, reflecting the greater efficiency of this pollination system.

While autogamy predominates in the genus, morphological evidence and field observations demonstrate that outcrossing also occurs. In the outcrossing taxa, the petals are conspicuous, nearly planar at anthesis, and may provide a suitable platform for insects. The large number of anthers and the echinate pollen insures that any suitable insect visitor will receive some grains. In addition, the stigmas are generally papillose and this may aid in the efficient attachment of the grains when they are transferred. The generally large number of apertures on the grains perhaps insures germination at various orientations on the stigma. Since nectar is produced in minute amounts, the flower visitors are apparently attracted to the large amounts of pollen. This is supported by observations of pollen-gatherers on local species (see below).

Insect vectors

The three Texas species *M. americanum, M. aurantiacum,* and *M. coromandelianum* were observed in the field, and flower visitors were captured. In my two years of observation, insect pollinators or potential pollinators were never seen in the flowers of *M. coromandelianum* in Texas, but *M. americanum* flowers were occasionally visited by a large number and variety of insects. In mid-October, 1978, I collected a group of insects from flowers of the northernmost population of this species known in Texas (at Corpus Christi). A list of these insects as well as others appears in Table 2. All are widespread generalized foragers except for the weevil *Anthonomus solarii* which is also known from *M. coromandelianum* along with *A. squamans* which appears to feed upon the flower buds (Burke, 1968). The former not only feeds upon the pollen but also completes its life cycle as a larval parasite in the fruits. The ants and butterfly

Table 2. **Pollinators and Predators**

Insect	Species utilized	Part utilized	Voucher plant or reference
Acanthoscelides cf. *aequalis* Sharp (Coleoptera: Bruchidae)	*M. americanum*	mericarps	*Seymour 2362*
Anthonomus solarii Champion (Coleoptera: Curculionidae)	*M. americanum*	pollen, buds	*Hill 8093;* Burke, 1968
Anthonomus squamans Champion (Coleoptera: Curculionidae)	*M. americanum* and *M. coromandelianum*	young mericarps, buds	*Hill 6054;* Burke, 1968
Apion sp. (Coleoptera: Curculionidae)	*M. americanum*	mericarps	*Chippendale 7148; Johnson 2116*
Celotes limpia Burns (Lepidoptera: Hesperiidae)	*M. americanum*	foliage	Burns, 1974
Cochliomyia macellaria Fabr. (Diptera: Calliphoridae)	*M. americanum*	pollen	*Hill 8093*
Halictus ligatus Say (Hymenoptera: Halictidae)	*M. aurantiacum*	pollen	*Hill 4514*
Lerodea eufala Edw. (Lepidoptera: Hesperiidae)	*M. americanum*	nectar?	*Hill 8093*
Macrorhoptus sp (undescr.) (Coleoptera: Curculionidae)	*M. aurantiacum*	pollen, mericarps	*Hill 4514;* Burke, 1973
Megabombus pennsylvanicus De Geer (Hymenoptera: Apidae)	*M. americanum*	pollen	*Hill 8093*
Megachile montivaga Cresson (Hymenoptera: Megachilidae)	*M. americanum*	pollen	*Hill 8093*
Monomorium minimum Buckley (Hymenoptera: Formicidae)	*M. americanum*	nectar?	*Hill 8093*
Strymon melinus Hubner (Lepidoptera: Lycaenidae)	*M. coromandelianum*	young mericarps, foliage?	*Hill 5112*
Vanessa caryi (Lepidoptera)	*M. tomentosum*	foliage	*Smyth 48*

collected on the flowers were apparently the only insects feeding upon the nectar. Flowers of *M. aurantiacum* were visited by fewer individuals and fewer species of insects (listed in Table 2). The insects observed were feeding upon and gathering the pollen and made no attempt to search out the poorly-developed nectaries. The undescribed species of *Macrorhoptus* was seen in Brazos County and Goliad County on *M. aurantiacum* and completes its life cycle as a larval seed-parasite within the fruits. Some benefit may be gained by both members of this symbiosis, since pollen may be transferred by the insect. I feel that it is significant that *Macrorhoptus* is also known from Argentina (Burke, 1973) where *M. aurantiacum* is thought to have originated, suggesting an ancient association.

Several Bruchid weevils have been found as parasites in the fruits of *M. americanum* in Central America and Australia. While lepidopterids are infrequent visitors to *Malvastrum*, several are known to utilize the foliage. *Vanessa carvi* larvae feed on the foliage of *M. tomentosum* in Peru (field notes from *Smyth 48*) and *Celotes limpia* will feed upon *M. americanum* in the laboratory (Burns, 1974). Other larval predators were collected on *M. coromandelianum*.

In summary, primary pollination-vectors seem to be pollen-gathering solitary bees and Anthonomid weevils.

COMPARATIVE MORPHOLOGY

Although several of the species of *Malvastrum* have been well known (under various names) for a considerable time, descriptions of certain morphological details that are of diagnostic value are usually lacking in the literature. In particular, vesture characters, seen to be exceedingly useful diagnostic features in this study, have been detailed only infrequently, such general terms as 'strigose', 'hispid', and 'tomentose' being the only commonly used terms. No detailed study of stamen number in the genus has come to my attention except for those pointing out unusually low numbers in some taxa (see Krapovickas, 1957b). Petal-shape, vesture of the stamen column, and mericarp number have been only cursorily examined in the past in the genus. I have examined the variation in over 80 characters for this study and have used 60 of these in a numerical analysis to prepare a graphic presentation of the cladistics of *Malvastrum* using the Wagner Groundplan/Divergence Method

(see Fig. 18). This section summarizes the variation within *Malvastrum* and is based upon data obtained from herbarium specimens, field observations, and cultivated individuals grown at College Station, Texas.

Habit and duration

Members of the genus *Malvastrum* are mostly characterized by a suffrutescent or nearly fruticose perennial habit with herbaceous stems that may become soft-woody in age. Several species are annuals in disturbed situations, and one (*M. hispidum*) is always annual. Nevertheless, all the taxa produce strong fibrous to soft-woody tissues as they mature. The perennials occasionally die back or are grazed back to a ligneous branched caudex at ground level and produce new growth from it. Other perennial species may produce new growth from erect woody stems. While it is not known precisely how long the plants may live, I have collected *M. americanum* wood samples in Texas (*Hill 7640*) that bore six annual rings. All of the taxa under cultivation reached reproductive maturity in a single year with a constant adequate water supply. Vegetative growth is seasonal in the greenhouse due in part to a normal dormancy exhibited by the species. The individuals grown locally in the greenhouse equalled or exceeded heights attained by individuals in the wild in a single season, varying from 20 cm (*M. coromandelianum* subsp. *coromandelianum* and *M. hispidum*) to nearly 3 meters (*M. americanum*). Most of the species grow to a height averaging 1 meter.

Roots

Malvastrum roots take the form of a single or branched elongated taproot which may develop several somewhat fibrous lateral branches. The length of the root varies from 5–10 cm in the annuals to 0.5–1 meter below the soil surface in the strong perennial *M. aurantiacum* in which the length equals or exceeds that of the above ground parts.

The root system of *M. aurantiacum* is among the most rapid to elongate in the seedling stage (of those taxa examined) and at maturity consists of a single thickened somewhat fleshy taproot with a few small primary branches (Fig. 4c) and has a distinctive salmon-pink internal color. Some collections of *M. coromandelianum*

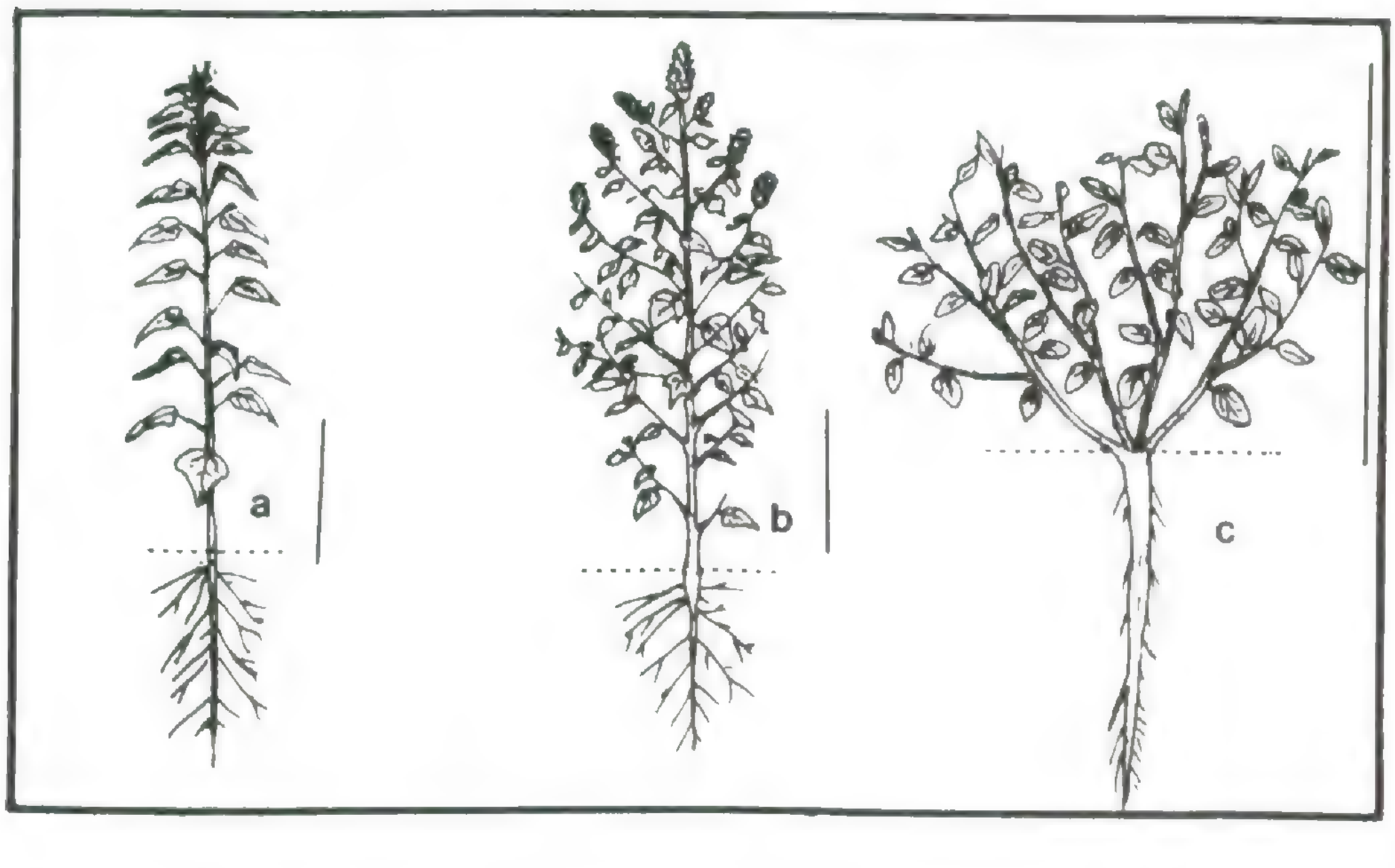


Figure 4. Habit variation in *Malvastrum*. a. *M. interruptum*, b. *M. americanum*, c. *M. aurantiacum*. Scale = 0.5 m.

subsp. *coromandelianum*, especially those from Texas and northern Mexico from semi-xeric or grazed areas, occasionally bear a similar but less fleshy unpigmented taproot. The other taxa for which roots are available have rather tough, ligneous, and more highly branched taproots that are usually less than half the length of the above ground parts (Fig. 4a & b). The root morphology in *Malvastrum*, then, falls into two basic categories which correlate loosely with habitat: 1) taxa with somewhat thickened, elongated, sparsely branched taproots (in periodically wet and poorly drained soils, which may seasonally dry to a parched state), and 2) those with less thickened, comparatively short, and more highly branched taproots (in well-drained soils). Except for the limited variation discussed above, the root-systems are of little diagnostic value in *Malvastrum*.

Vesture

The variation in hair types and their distribution is second in importance only to characters of the mericarp in recognizing the taxa of *Malvastrum*. The usual multiradiate stellate hair of the Malvaceae has been modified in various ways and usually independently within the genus. While not very useful in separating genera within the family, variation in vesture can aid in distinguishing species within genera when each taxon has a unique combination of

hair types. While variable in other genera (such as *Malvaviscus* Adanson and *Anisodontea* Presl, see Bates, 1969) general patterns of vesture are nearly constant within the species of *Malvastrum* allowing the determination of vegetative specimens with a degree of confidence.

Modification of the basic stellate hair has apparently proceeded in several directions within the genus (Fig. 5). The basic or primitive hair type in the genus is taken to be the 5–8-rayed, somewhat tufted to nearly rotate, actinomorphic, multicellular, slightly tuberculate stellate hair (Fig. 5a) found in all of the taxa but nearly lacking in some (*M. aurantiacum, M. coromandelianum*). From the primitive hair can be derived the 10–12-rayed, often biseriate, tufted stellate hair (Fig. 5b), perhaps by the multiplication of basal precursor cells during development. Probably functioning in semi-arid regions as a windscreen, this hair type in *Malvastrum* is most frequent on abaxial leaf surfaces, a surface where the stomata are concentrated. This 10–12-rayed hair is absent from *M. aurantiacum, M. bicuspidatum* (except subsp. *oaxacanum*), *M. chillagoense, M. corchorifolium, M. coromandelianum,* and *M. hispidum*. Probably also from the basic type has been derived the appressed (6) 8–10-rayed pseudolepidote stellate hair. This hair type with basally coalesced rays is found only in *M. aurantiacum* (Fig. 5c).

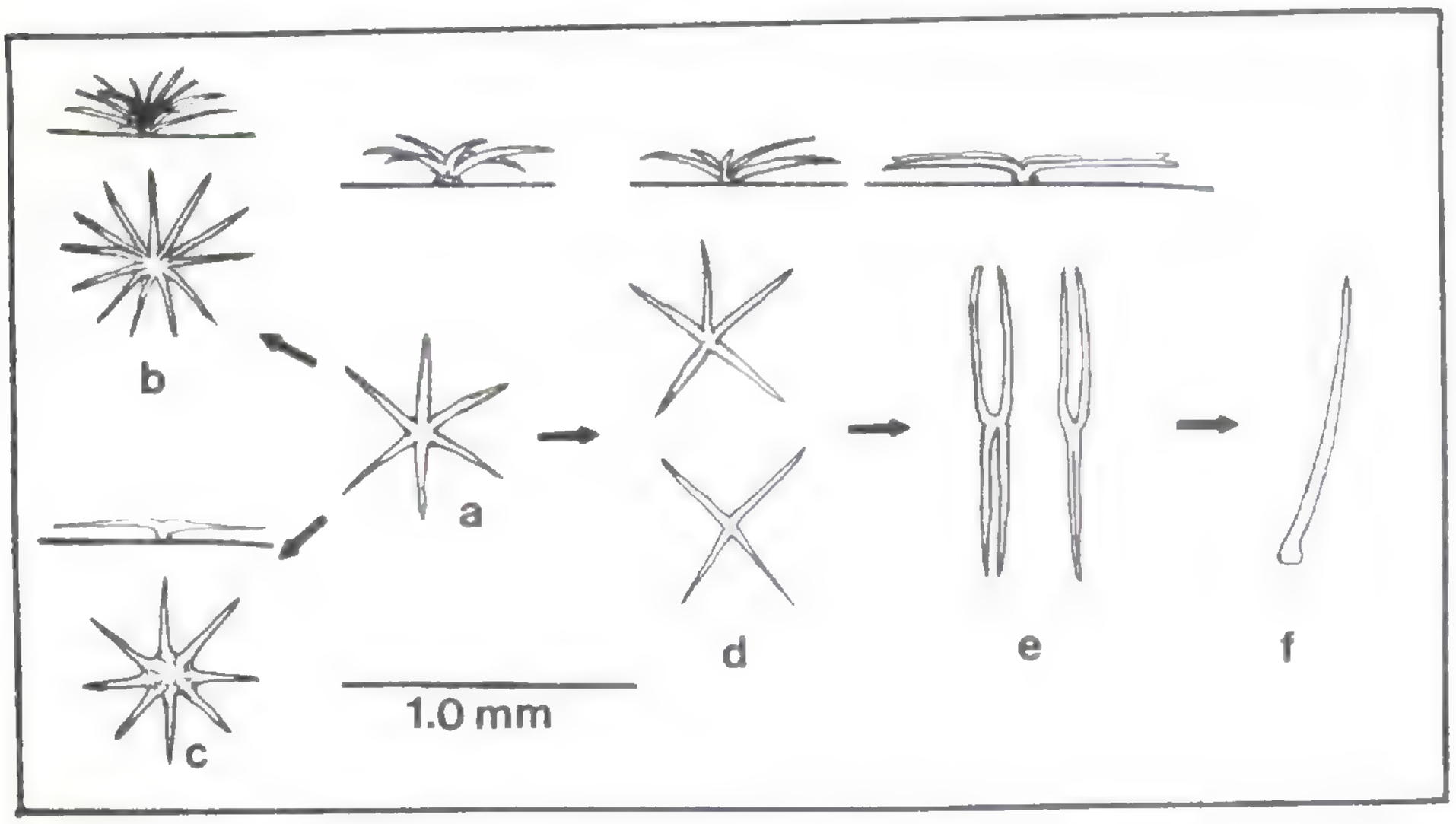


Figure 5. Elaboration or reduction of stellate hairs in *Malvastrum*. a. Unspecialized tufted 6-rayed hair. b. Multiplication of rays. c. Planation and coalescence of rays. d. Reduction of rays. e. Reduction, planation, and change in symmetry. f. Simple hair.

A third derivation pattern involves a reduction in the number of rays and a subsequent change in the symmetry of the hair. Several taxa have 4–5-rayed actinomorphic stellate hairs with equally divergent rays (Fig. 5d) and others have hairs which show a trend towards bilateral symmetry. This trend reaches its peak development in *M. corchorifolium* and *M. coromandelianum*. These two species bear closely appressed, bilateral, thickened, 4-rayed stellate hairs (the "H-shaped stellate hair" of Rao and Ramayya, 1977), which often have contiguous parallel rays directed longitudinally on plant parts (Fig. 5e). Similar hairs occur in other Malvaceae such as *Hibiscus coulteri* Harv. ex Gray and *Sida ciliaris* L. These hairs are infrequently reduced to submalpighiaceous hairs with 2 or 3 rays.

The final reduction of the basic stellate hair to a simple hair has occurred independently in several taxa and on various plant parts. The simple hairs may arise from a multicellular base or may be unicellular but in both cases arise from the epidermis (Fig. 5f).

Rao and Ramayya (1977), in describing the trichomes of *M. americanum* and *M. coromandelianum* in India, point out several hairs that they term "flagellate hairs", which are restricted to the adaxial surface of the calyx lobes. In my species descriptions I have referred to these as arachnoid hairs. These are all minute (ca. 150–250 μm) simple or stellate hairs with thin walls and flexible rays and are found in most of the taxa on the adaxial surface of the calyx lobes and bracteoles, and less frequently on the adaxial surface of the stipules.

Glandular hairs are lacking in *Malvastrum* except for the multicellular nectar-secreting hairs of the internal basal surface of the calyx. These are found in restricted regions beneath and between the petal claws.

The vesture attributes to the plant parts a texture varying from velvety to scabrous to nearly smooth. Most of the hairs are colorless, vitreous, and rigid at maturity (with the exception of the glandular and arachnoid hairs) but do not penetrate skin. In one taxon of the genus (*M. bicuspidatum* subsp. *tumidum* var. *glabrum*) all vesture has been lost on the fruit. In the other taxa the aboveground vegetative and reproductive parts with the exception of the anthers, style, and stigma, and occasional exception of the filament tube have at least some vesture.

The size of the hairs in *Malvastrum* is quite variable. The smallest glandular nectary hairs measure ca. 50 150 μm and the largest

simple and 4-rayed bilateral hairs of *M. coromandelianum* may reach a length of 2.0 mm. Most hairs are 0.5–1 mm in diameter in the genus. Hairs of different sizes are often mixed.

There are probably several important functions attributable to the hairs. In addition to protecting the plant from water loss, the hairs on the flower buds, ovaries, and soft vegetative parts may discourage insect predation. In *Gossypium* it is known that resistance to leafhoppers (family Jassidae) is dependent upon the density of the vesture on the abaxial surface of the leaf (Knight, 1952). In rice (Martins et al., 1977) it is known that more pubescent varieties discourage oviposition by predators. The bristle-like hairs on the mericarps in some taxa may aid in their adherence to fur and so in their dispersal.

The density of the vesture of any given plant depends not only on genetics, but also upon the age of the plant part and the habitat. Young herbaceous plant parts bear a very dense indument of overlapping hairs that becomes less dense as the tissues enlarge and lignify. Plants growing in moist areas and in shade have a more sparse vesture than those in dry or exposed areas. This suggests that hairs may also function to decrease the incident light to the leaf surface as well as to protect it from water loss. The vesture in *Helianthus, Tussilago,* and *Encelia* is known to reflect selectively as much as 56 percent of certain light spectra (Gousman et al., 1977; Eller & Willi, 1977; Ehleringer et al., 1976).

Stems

The stems have a moderate pith, a siphonostelic vascular cylinder, a chlorenchymatous cortex in youth, and a well-developed epidermis from which the vesture arises. The stem increases as secondary tissues are produced to a basal diameter of 1–15 mm. The green pigment is lost for the most part as secondary tissues such as cork arise and the stem becomes narrowly furrowed longitudinally. The hairs may or may not persist. In regions of seasonal variation, annual growth rings may be produced, while in temperate regions the stems generally die back to ground level or to the main stem in winter.

The branching pattern is monopodial. In the seedling stage all species in cultivation produce a single actively growing main stem that later produces few to several primary branches. In some taxa the main stem retains its dominance and primary branching occurs

only after injury, as inflorescences are produced, or in the second year (as in *M. interruptum* and *M. spiciflorum*, Fig. 4a). In a second group of taxa (such as the sections *Amblyphyllum* and *Tomentosum*, *M. americanum*, and *M. coromandelianum* subsp. *capitatospicatum*) branches are regularly produced as the plant reaches maturity but the main axis retains its dominance and secondary branching is infrequent (Fig. 4b) unless the main axis is damaged. The third branching pattern is seen in *M. aurantiacum* and *M. coromandelianum* subsp. *coromandelianum* in which the main axis in the young plant soon loses its dominance and several primary branches, often basal, achieve the same stature. In these two taxa secondary branching is frequent (Fig. 4c). In each succeeding year several main stems are produced from the ligneous crown.

Cotyledons

The cotyledons of those taxa examined are ovate with a subcordate truncate to wide-cuneate base and a retuse to rounded apex. The margins are entire, but in *Malvastrum amblyphyllum* and *M. grandiflorum* (Fig. 6a) the cotyledon has a tendency to be very briefly three-lobed in the apical third. The petiole in all of the taxa examined is puberulent with simple to 2-rayed erect hairs less than 0.5 mm long and the blade is glabrous to minutely ciliate at the basal margin. Each cotyledon has a midnerve and 2 or 4 additional palmately arranged veins and few secondary veins. While subequal in length and width or even wider than long in most taxa, the blades of *M. aurantiacum* (Fig. 6b) and *M. hispidum* cotyledons are slightly longer than wide and easily recognizable. The three cotyledon types are presented in Fig. 6, the most frequent form represented by *M. coromandelianum* (Fig. 6c). The cotyledons measure (6)7–18 mm in length, (7)8–13 mm in width, and their petioles are 3–9 mm long.

Leaves

As in many genera of the Malvaceae, the leaves of *Malvastrum* are spirally arranged, petiolate, basically ovate with a tendency to be briefly 3-lobed, cordate truncate to wide-cuneate at the base, and acute acuminate or rounded at the apex, have a single midvein and several associated palmate veins, are marginally dentate to dentate-serrate, and bear paired lateral stipules at each node. The leaf form

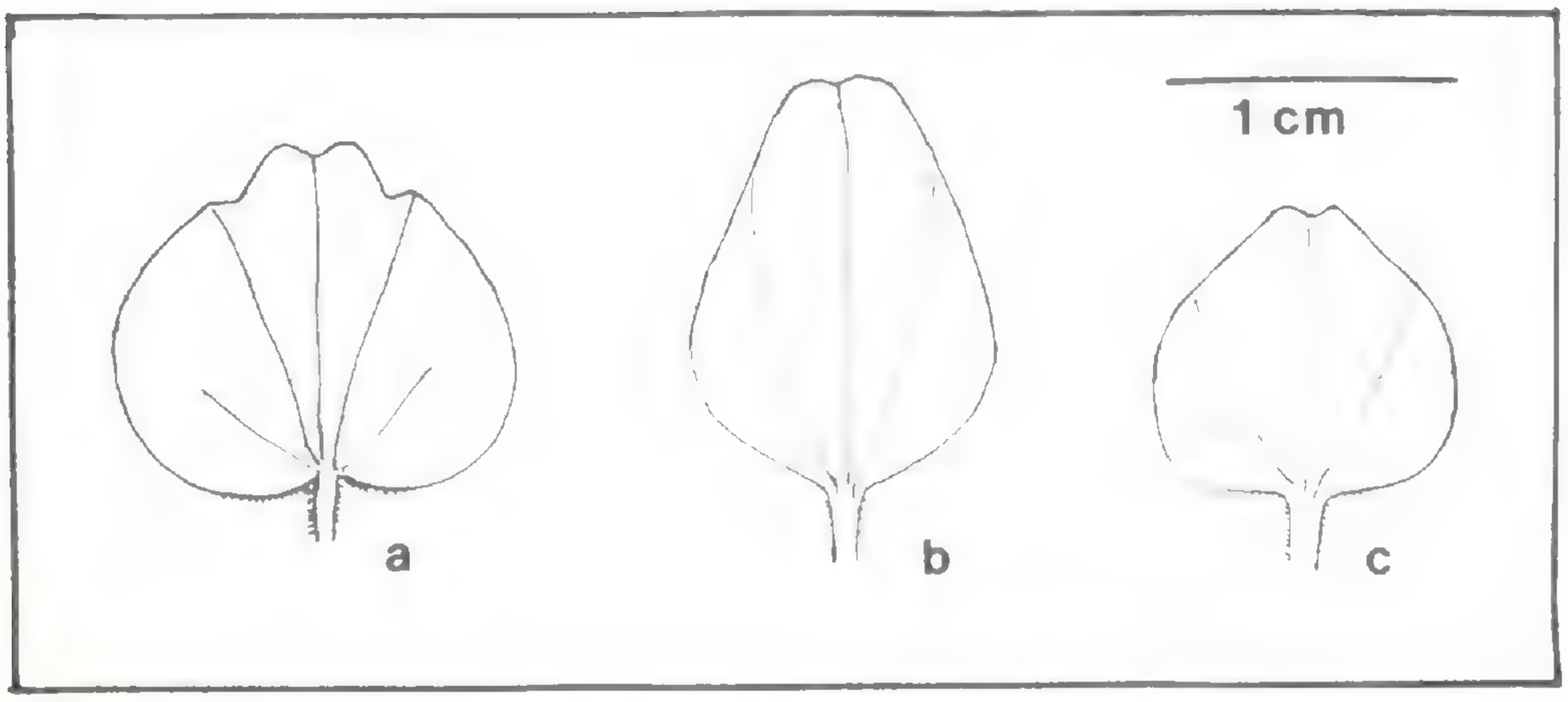


Figure 6. Cotyledon variation in *Malvastrum*. a. *M. grandiflorum (Krapovickas 19300).* b. *M. aurantiacum (Hill 6430).* c. *M. coromandelianum (Hill 4579).*

varies according to the taxon and the placement on the stem. Figure 7 exhibits some of the variation in leaf morphology found in the genus.

The petioles, (3)5–50 (100) mm long, are longest in early vegetative leaves, reduced apically, and are pubescent with hairs resembling those of the stem. They may subequal the blades or be 1/6 their length or less. The blades may or may not vary in form corresponding to their placement on the plant. In *Malvastrum amblyphyllum* (Fig. 7a), *M. aurantiacum, M. corchorifolium,* and *M. hispidum* (Fig. 7b), the blades scarcely vary with placement except that the earliest blades are often slightly larger or wider than those produced late in the season. In addition, the blades of these four species are almost always unlobed. Leaves of the remaining taxa are variable to a limited degree in size and shape in a manner similar to those of *Anisodontea* Presl studied by Bates (1969). The mature vegetative leaves produced on the main stems during the periods of most active seasonal growth are the largest, particularly in first-year plants. These early vegetative leaves vary from 2.5 3.5 cm long × 0.5-0.9 cm wide in *M. hispidum* to 5.0 11.5 cm long × 4.0–10.0 cm wide in *M. americanum* (Fig. 7c). In mature plants the blades and petioles are smaller and narrower, especially in *M. americanum* (Fig. 7d), *M. bicuspidatum,* and *M. coromandelianum* subsp. *capitato-spicatum.* The final leaves produced with the inflorescence are the smallest, nearly sessile in some cases (petioles 5 mm or less in length), and often unlobed or with highly reduced lobes. At the time of

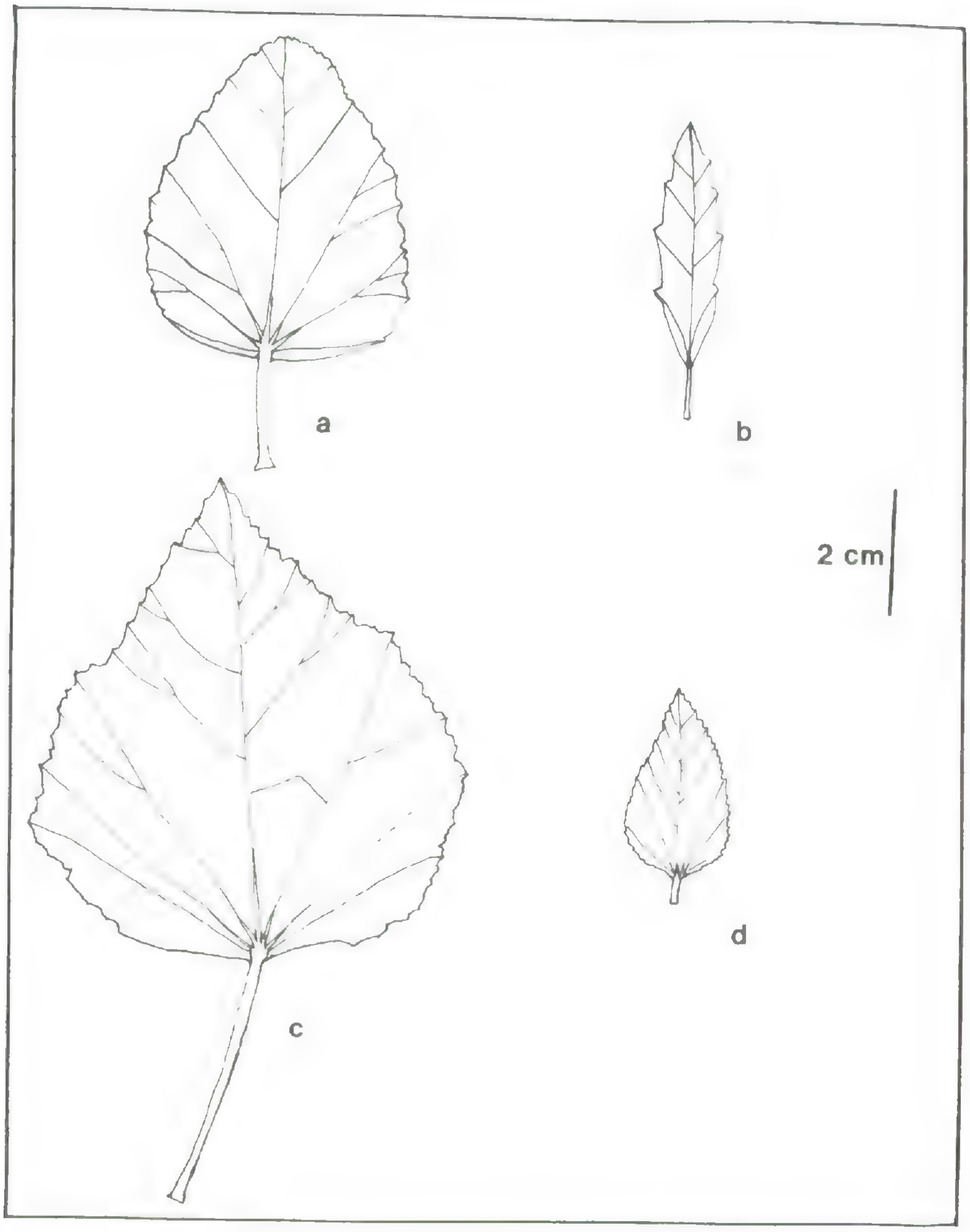


Figure 7. Leaf variation in *Malvastrum*. a. *M. amblyphyllum (Krapovickas 19127)*. b. *M. hispidum (Bates 2691)*. c. & d. *M. americanum (Krapovickas 15566)*.

reproductive maturity nearly all of the large main stem leaves have fallen, probably as an adaptation to drying conditions and a result of lessened metabolic activity. As also noted in *Anisodontea* Presl (Bates, 1969, p. 260–265) immature individuals of *Malvastrum* are different in appearance from those at reproductive maturity due to changes in both the branching pattern and in leaf morphology.

The orientation of the leaves on the midstem region of the main stem was examined for potential diagnostic value. Measurements of the angle formed between the petiole and the stem above were taken from cultivated specimens at midday since it was noted that the leaves droop at night as well as in age, changing the angle. This study was undertaken after the narrow angle specific to *M. interruptum* (and possibly also *M. spiciflorum*) was observed. The angle was seen to vary from 30°–60° in *M. interruptum,* to 90° in *M. amblyphyllum,* and to the usual 110°–113° in *M. americanum.* While of some diagnostic value in living vegetative plants, this character is not useful in pressed specimens.

The vesture of the leaves can be used to distinguish not only species but also subspecies, as in *M. bicuspidatum,* and in delineating specific populations, as in *M. coromandelianum.* All of the hair types described earlier in this work except for the arachnoid and glandular hairs are present in various combinations on *Malvastrum* leaf surfaces. The hairs are often best developed over the veins and these often have a greater number of rays than those in intercostal zones. The hairs may be reduced in size and number of rays towards the leaf margins.

The leaf venation is basically palmate in *Malvastrum.* The midnerve is the most strongly developed, and there are one to three additional pairs of nerves radiating from the base of the blade. The primary veins extend to the margins and terminate in the marginal teeth. Secondary veins branch from the primary veins and may terminate in the teeth. The smallest reticulate veins occur throughout the remainder of the leaf. The primary veins are conspicuously raised on the abaxial surface of the leaf in both fresh and dried specimens and slightly impressed above (except in *M. interruptum* in which they are deeply impressed on the adaxial surface).

The leaf-margins are typically dentate but may be crenate-dentate, nearly serrate, or denticulate. There is a tendency for the teeth to be relatively large and few in number/cm in the early main stem leaves and in leaves from shaded plants. The later leaves have

relatively smaller teeth and a larger number/cm of margin (e.g., in *Malvastrum americanum* var. *americanum* main stem leaves have 2 teeth cm, increasing to 7 teeth/cm in apical leaves). Taxa from more arid regions show a tendency towards serrate leaf margins particularly on those leaves produced late in the season (e.g. *M. bicuspidatum* and certain populations of *M. coromandelianum*).

Lobing of the blade is poorly developed in *Malvastrum*. The lobes are less than 1 cm deep and often appear as a pair of enlarged teeth about 1/2 to 2/3 the distance from the base of the blade, each with the terminus of an elongated palmate vein. Most of the taxa retain leaf lobing only in the juvenile leaves, if at all, suggesting that lobing is a primitive feature within the genus.

Stipules

Malvastrum stipules are found paired at the base of the petioles or, less frequently, subtending the flowers. The shape varies from wide-lanceolate (Fig. 8a) to narrowly triangular (Fig. 8b) to nearly linear (Fig. 8c), and the stipules are usually falcate, widest at the base, and have a long-acuminate to subulate apex. They are completely free from the petioles. The length varies from 2–16 mm and the width from 0.2 1.5 mm. The stipules are often reduced in the congested axillary inflorescences of *M. coromandelianum* subsp. *capitato-spicatum*, *M. interruptum*, *M. spiciflorum*, and *M. tomen-*

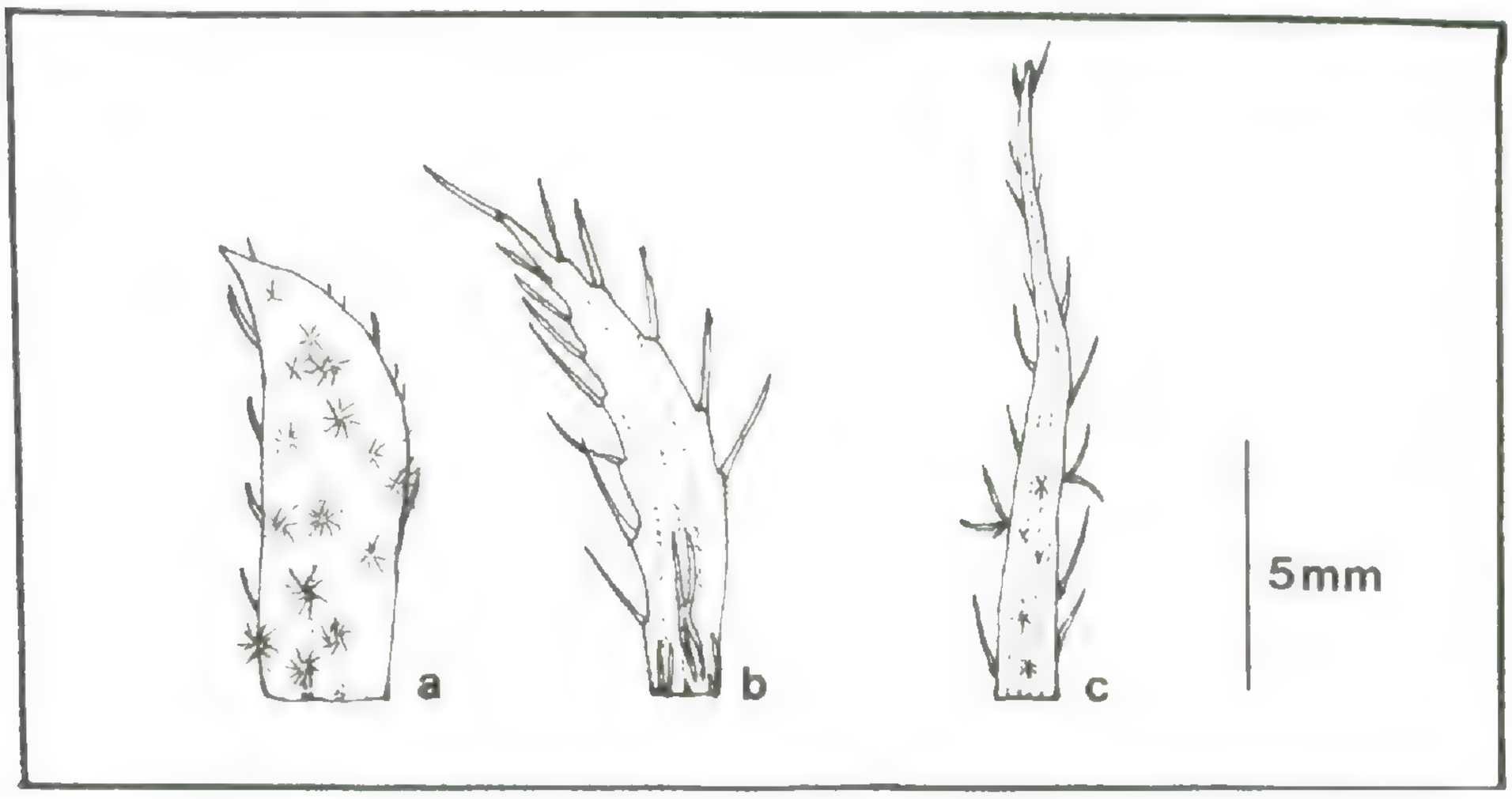


Figure 8. *Malvastrum* stipules. a. *M. aurantiacum (Hill 6430).* b. *M. coromandelianum (Hill 4579).* c. *M. grandiflorum (Krapovickas 19300).* Abaxial surface views.

tosum, but are retained unchanged or as modified floral bracts in the other taxa. The stipules remain green or may dry within a few days. They may be early deciduous, may fragment gradually, or may persist, but this character can vary within a taxon. The stipules are appressed to the stem, perpendicular to the stem, or slightly reflexed. The stipular margin is entire to irregularly toothed, the dentition resulting from the development of large marginal multicellular based simple hairs (e.g. *M. coromandelianum,* Fig. 8b). The vesture of the stipule surface resembles that of the stem, usually consisting of appressed stellate and marginally simple hairs, and the adaxial surface is glabrous or has a few scattered stellate or arachnoid hairs. The venation of the stipules is usually obscure or consists of 1–5 palmate veins that become parallel immediately above their base.

Inflorescence

There are four related inflorescence-types in *Malvastrum,* the simplest consisting of solitary flowers in the axils of leaves and their associated stipules (Fig. 9a). The flowers produced late in the season may appear congested at the apices of the stems when the internodes are reduced. Taxa with this inflorescence-type exclusively include *M. amblyphyllum, M. aurantiacum, M. coromandelianum* subsp. *coromandelianum, M. grandiflorum,* and *M. hispidum.* In young

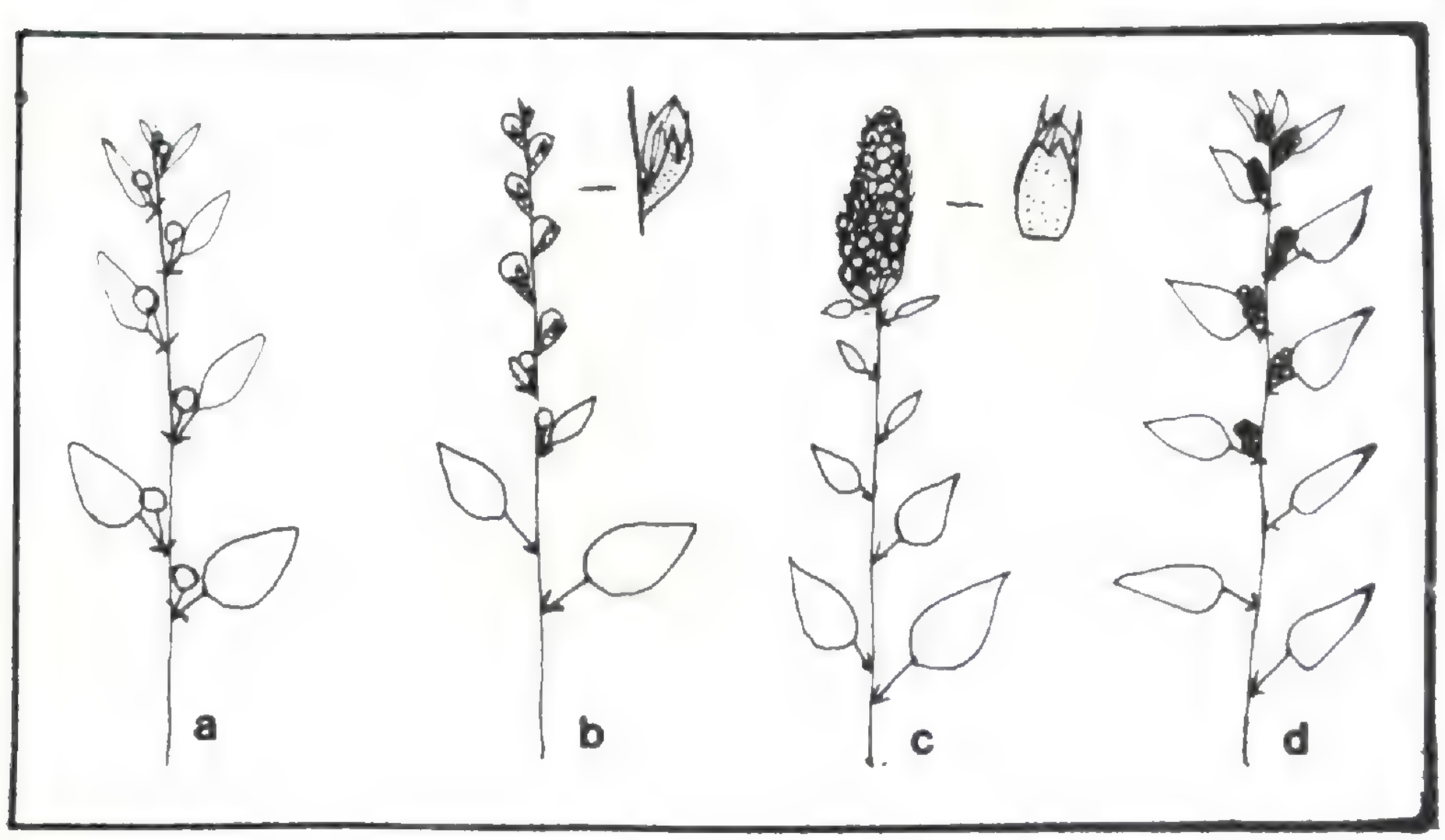


Figure 9. Inflorescence types in *Malvastrum.* a. Solitary, axillary. b. Terminal raceme. c. Terminal spike. d. Axillary spicate racemes. Schematic.

plants of most other taxa the first flowers are produced in this manner, but the inflorescence soon becomes more complex.

The second inflorescence-type is a simple terminal raceme (Fig. 9b). This raceme, if present, generally terminates every branch-apex and the flowers are either non-continuous with long (0.5–2 cm) internodes or congested and subspicate. The flowers are pedicellate (pedicels 0.5–2 mm long in flower) and at least a few lack subtending leaves. They are usually subtended instead by a sessile bifid bract derived by partial connation of the paired stipules. This inflorescence type is found exclusively in *M. bicuspidatum* (all subspecies), *M. chillagoense, M. coromandelianum* subsp. *fryxellii, M. guatemalense,* and *M. scoparioides.*

The third inflorescence-type is closely allied to the last and can be called a congested terminal spike (Fig. 9c). The flower pedicels are nearly absent, the flowers are densely congested at the apex of all upper branches (which are leafy below), and each flower is subtended by a bifid bract. This type is found exclusively in *M. americanum* and in mature individuals of *M. corchorifolium.* Several other taxa have congested inflorescences that superficially resemble those of *M. americanum,* but these can easily be distinguished by the lack of bifid bracts, the presence of subtending floral leaves, or by the lack of leaves in the lower part of the reproductive branch.

The fourth type of inflorescence consists of a number of short (1–4 cm) leafless axillary spicate racemes located in the upper half to third of the plant (Fig. 9d). This inflorescence-type probably has been derived independently in several taxa. The floral bracts usually consist of reduced, paired stipules that are rarely united in their basal half to form a bifid bract. The pedicels are 0.5–1.0 mm long. Each inflorescence unit is in the axil of an upper or midstem leaf that usually exceeds it. A terminal congested spicate inflorescence composed of several of the smaller inflorescence units with reduced leaves and internodes between is usually present in fully mature individuals. This type of inflorescence is found exclusively in *M. coromandelianum* subsp. *capitato-spicatum, M. interruptum, M. spiciflorum,* and *M. tomentosum.* To a certain extent, *M. bicuspidatum* subsp. *tumidum* and *M. guatemalense* have a reduced but basally leafy racemose inflorescence approaching this type.

Ideas concerning trends in the evolution of the inflorescence in *Malvastrum* are based on inductive reasoning. I have assumed that

the most primitive type is that consisting of solitary axillary flowers as in most other members of the Malvaceae and that the other types with reduced internodes, united stipules, or reduced to absent leaves have been derived from this. Evidence for this is seen in the fact that every taxon has at least one or two early solitary axillary flowers before the inflorescence becomes more complex. However, there is the possibility that through neoteny, a delay in the development of adult characteristics, the solitary axillary inflorescence can recur. This may explain, in particular, the solitary axillary flowers in *M. coromandelianum* subsp. *coromandelianum* which produces somewhat congested terminal inflorescences only at full maturity or senescence. Therefore, there is no reason to suppose that inflorescence evolution is unidirectional in *Malvastrum*.

The bifid floral bracts that have been used in the past (Krapovickas, 1957b) to distinguish *M. americanum* from other taxa with congested inflorescences are actually found in several other species as well. Morphological and developmental evidence from both herbarium specimens and greenhouse plants shows that the bifid floral bracts found in members of the genus are derived from paired leaf stipules. In many individuals a progression can be clearly seen from well-developed leaves with their associated stipules, to reduced leaves with stipules, stipules with a leaf remnant attached, and finally to a bifid bract (Fig. 10). The bracts are best developed in *M. americanum* (Fig. 10d) and are present to a significantly lesser degree in the other taxa. Developmental progressions are best seen in *M. corchorifolium* (Fig. 10b-c) and *M. bicuspidatum*. In many respects, the bracts of *M. corchorifolium* are intermediate between the paired stipules in *M. coromandelianum* (Fig. 10a) and the bifid bracts of *M. americanum*.

Involucel

The involucel (epicalyx) of the individual flowers of *Malvastrum* is always composed of three distinct bracteoles. These are arranged in a more or less spiral manner either at the pedicel-calyx juncture or are adnate to the calyx at various levels. In exceptional cases one or more bracteoles may be slightly remote on the pedicel. The bracteoles vary in shape from the unusual deltate-cordiform structures seen only in *M. aurantiacum* (Fig. 11a), to the more frequent lanceolate bracteoles of *M. coromandelianum* (Fig. 11b), and finally to the linear or filiform shape seen in *M. tomentosum* (Fig. 11c) and

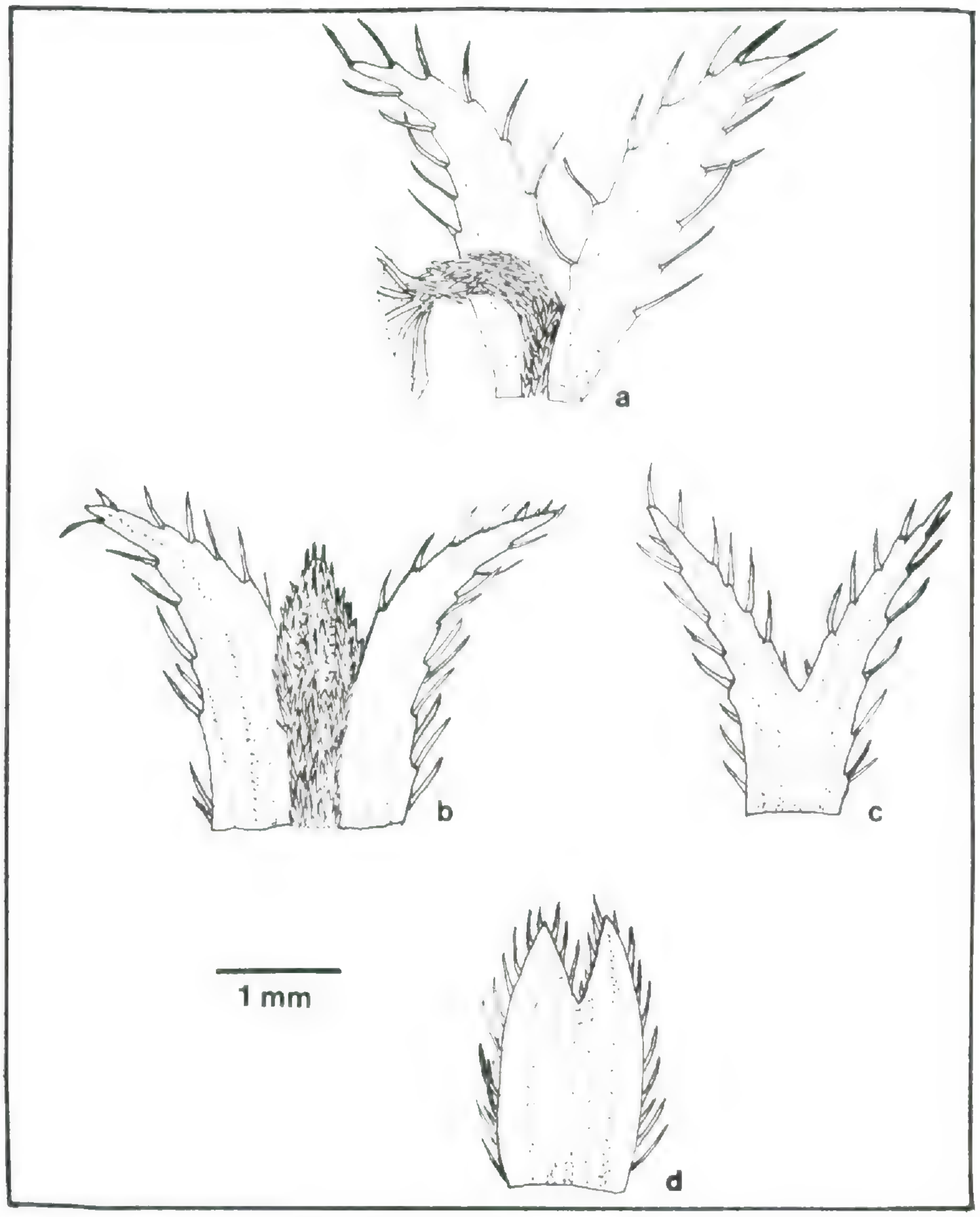


Figure 10. Evolution of the bifid floral bract in *Malvastrum*. a. Stipules of *M. coromandelianum (Curtiss 6421)*. b. Leaf vestige (mature state) and adnate stipules *M. corchorifolium (Correll & Evans 44026)*. c. Bifid bract *M. corchorifolium (Molina 23070)*. d. Bifid bract, *M. americanum (Ventura 2622)*. Adaxial surfaces.

others. On occasion the bracteoles are slightly falcate. The vesture, venation, and, to a lesser degree, the shape strongly resemble corresponding characters of the stipules and suggest a homology with those structures.

The bracteoles usually extend one-third to one-half the length of the calyx lobes in flower. Less frequently they extend to the lobe sinus (as in *Malvastrum aurantiacum, M. bicuspidatum* in part, and *M. hispidum*) or equal or exceed the calyx lobes (as in *M. americanum, M. corchorifolium, M. grandiflorum,* and *M. interruptum*). The bracteole length in relation to the calyx-lobes can be of value in distinguishing species, but is not particularly useful at the sectional level in *Malvastrum*. The length of the bracteoles varies from 2–3 mm in *M. spiciflorum* and some individuals of *M. hispidum* to a maximum of 18 mm in *M. grandiflorum,* averaging 4–8 mm. The width varies from 0.2–0.3 mm in *M. spiciflorum* and *M. tomentosum* to a maximum of 5 mm in *M. aurantiacum,* averaging 0.5–1.0 mm. While usually free or united to the calyx for less than 1 mm, the bracteoles are united to the calyx for as much as 2–3 mm in *M. aurantiacum.*

The bracteoles are erect and appressed in bud, are spread out as the calyx expands in fruit, but usually do not reflex. They possibly function along with the floral bract and vesture to protect the young flower buds from both water loss and predation.

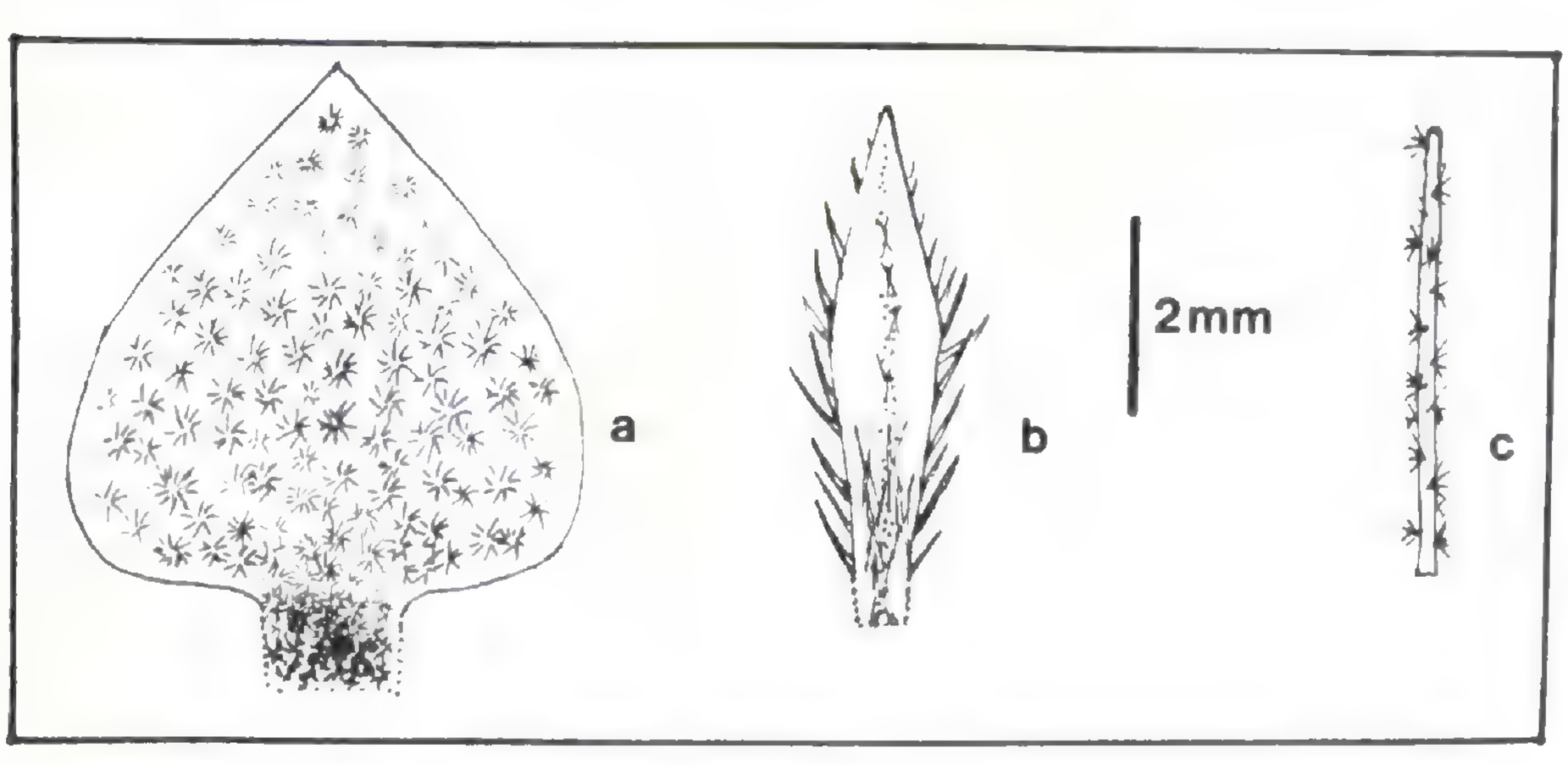


Figure 11. Involucellar bracteoles in *Malvastrum*. a. *M. aurantiacum (Fryxell 1314).* b. *M. coromandelianum (Breedlove 20019).* c. *M. tomentosum (Stark 8973).* Adnate portions stippled.

Calyx

The calyx in *Malvastrum* is composed of 5 sepals that are valvate in bud and united from 1/5 to 3/5 but usually 1/3 to half their length. The basal united portion is campanulate and glabrous within except for the basal nectaries. The lobes are deltate to narrowly triangular, acute acuminate to nearly cuspidate at the apex, and (1.5) 4 8 (15) mm long × (1.5) 4–6.5 mm wide. The internal surface of the lobe is minutely pubescent marginally and in the upper half with arachnoid simple or stellate hairs. The external surface is pubescent, often densely so, with nearly the full range of hair types. Hairs of the calyx are of great diagnostic value since species-specific combinations are usually present.

The extent of lobing of the calyx and the length to width ratio of the lobes are too similar among the taxa to be of diagnostic value. The absolute length of the calyx from pedicel to lobe-apex is more useful, though also variable. The extremes at anthesis range from a minimum of 2.8 mm in *M. hispidum* to a maximum of 15 mm in *M. grandiflorum*. Since the calyx is usually somewhat accrescent by an additional 25%–75% in fruit it is important to indicate at what stage it is measured.

The venation of the calyx-lobes, while often obscure, is reticulate with usually 3–5 or up to 10 primary subparallel veins.

The orientation of the calyx-lobes in fruit is of great diagnostic value in some groups, such as in the subspecies of *Malvastrum bicuspidatum*, *M. coromandelianum*, and *M. tomentosum*. The orientation is, in most cases, correlated with the development of ornamentation of the fruit. Those taxa with rotate or spreading lobes often have mericarps with long distal-apical cusps and those with erect or incurved lobes often lack such ornamentation. Lobe-orientation, then, may also correlate with dispersal. Those fruits adapted for animal-transport are exposed for effective dispersal, and those not so modified are retained in the calyx cup for longer periods for gradual dispersal. Some taxa may have secondarily lost the rotate lobe orientation as a result of the disappearance of animal vectors within their ranges, as in several *M. bicuspidatum* subspecies, *M. coromandelianum* subsp. *capitato-spicatum* and subsp. *fryxellii*, *M. scoparioides*, and *M. tomentosum* subsp. *pautense*.

Corolla

The corolla of *Malvastrum* consists of 5 distinct petals united basally to the staminal column. The petals are strongly imbricate in bud. Aberrant flowers with 6 petals have been seen in cultivated specimens of *M. americanum* and *M. interruptum* but are of no diagnostic value. An 'ovary cup' is formed by the fusion of the petals and the lower staminal column. The petals have a short (0.5–2 mm) claw that lacks auricles at the base and which gradually widens into the main body of the petals. In shape, the petals are asymmetrically obovate and usually emarginate or unequally cleft as in many other genera of the Malvaceae, but those of *M. spiciflorum* are entire. The flowers are odorless.

The petals of *Malvastrum* are shades of yellow, varying from pale yellow to golden-yellow, yellow-orange, to pale orange. Those of the section *Tomentosum* in particular tend towards orange. The color, however, may vary slightly in intensity even within a taxon in different parts of its range, as in *M. coromandelianum* subsp. *coromandelianum*. In only one species, *M. grandiflorum*, the petal claws are red while the main body is golden-yellow, suggesting a greater attractiveness to insects.

The petals are elaborately vascularized with reticulate palmate veins that generally anastomose before reaching the margins. In this as well as shape they resemble to a remarkable degree the wings of certain insects.

In most taxa the petal claws are rather densely pubescent to ciliate-tufted along each margin with firm, simple or stellate hairs. These intermesh with those of adjacent petals obscuring the calyx below. This screen may serve to protect the delicate glandular nectary-hairs on the calyx in that region and to prevent the evaporation or thickening of the sparse nectar. In several cases the claw-hairs are very sparse and this may indicate a lack of dependence on nectar as an insect-attractant.

The size of the petals is occasionally of diagnostic value, but since they are fragile, mucilaginous, and usually last for only a few hours they are often not adequately preserved on dried specimens. They vary in length from a minimum of 2.0–3.0 mm in *Malvastrum hispidum* and *M. spiciflorum* to a maximum of 23 mm in *M. grandiflorum*. The width of the petals varies from a minimum of 1.5–2.0 mm in *M. hispidum* and *M. spiciflorum* to a maximum of 15

mm in *M. grandiflorum* and *M. aurantiacum*. Petal-size tends to correlate with the pollination mechanism. Autogamous species have the smallest petals occasionally subequal to the calyx and entomophilous species have the largest petals exceeding the calyx by as much as 8 mm. In several taxa, particularly in *M. bicuspidatum, M. corchorifolium,* and *M. coromandelianum* subsp. *capitato-spicatum* the petals are smaller on individuals approaching dormancy. This may also be the case in other members of the section *Tomentosum* as observed in herbarium specimens. This phenomenon is not conspicuous in the other taxa.

The orientation of the petals is variable and also seems to correlate with the pollination mechanism. Those species with rotate corollas are either known to be or suspected to be obligate or facultative outcrossers and those with campanulate corollas are suspected to be primarily autogamous (*M. amblyphyllum, M. chillagoense, M. corchorifolium* in part, *M. hispidum,* and *M. spiciflorum*). *Malvastrum corchorifolium* was seen to produce both rotate and campanulate corollas depending upon the time of year and position of the flower. *Malvastrum hispidum* is occasionally cleistogamous.

Androecium

The androecium of *Malvastrum* is composed of monadelphous stamens which usually arise (as seen in bud) from five groups of primordia (Van Heel, 1966). This five-ranked symmetry is retained at anthesis in *M. grandiflorum* and less frequently in *M. coromandelianum,* but for the most part is obscured by the densely packed nature of the anther cluster. The filaments are united into a slender column 1.0–7 mm in height and are free at their apex for an additional 0.5–2.0 mm. Each is terminated by a unilocular anther with a partially intrusive or incomplete septum. Two anthers occasionally terminate a filament, and bilocular or incompletely bilocular anthers are occasionally seen. The anthers are attached by the free portions of the filaments at various levels at the apex of the column, which is the same color as the corolla.

The filament-tube may be either glabrous or sparsely pubescent with minute 2–5-rayed stellate hairs similar to those of the petal claws. This character is diagnostic as variation rarely occurs within a taxon. For example, *M. aurantiacum, M. coromandelianum,* and

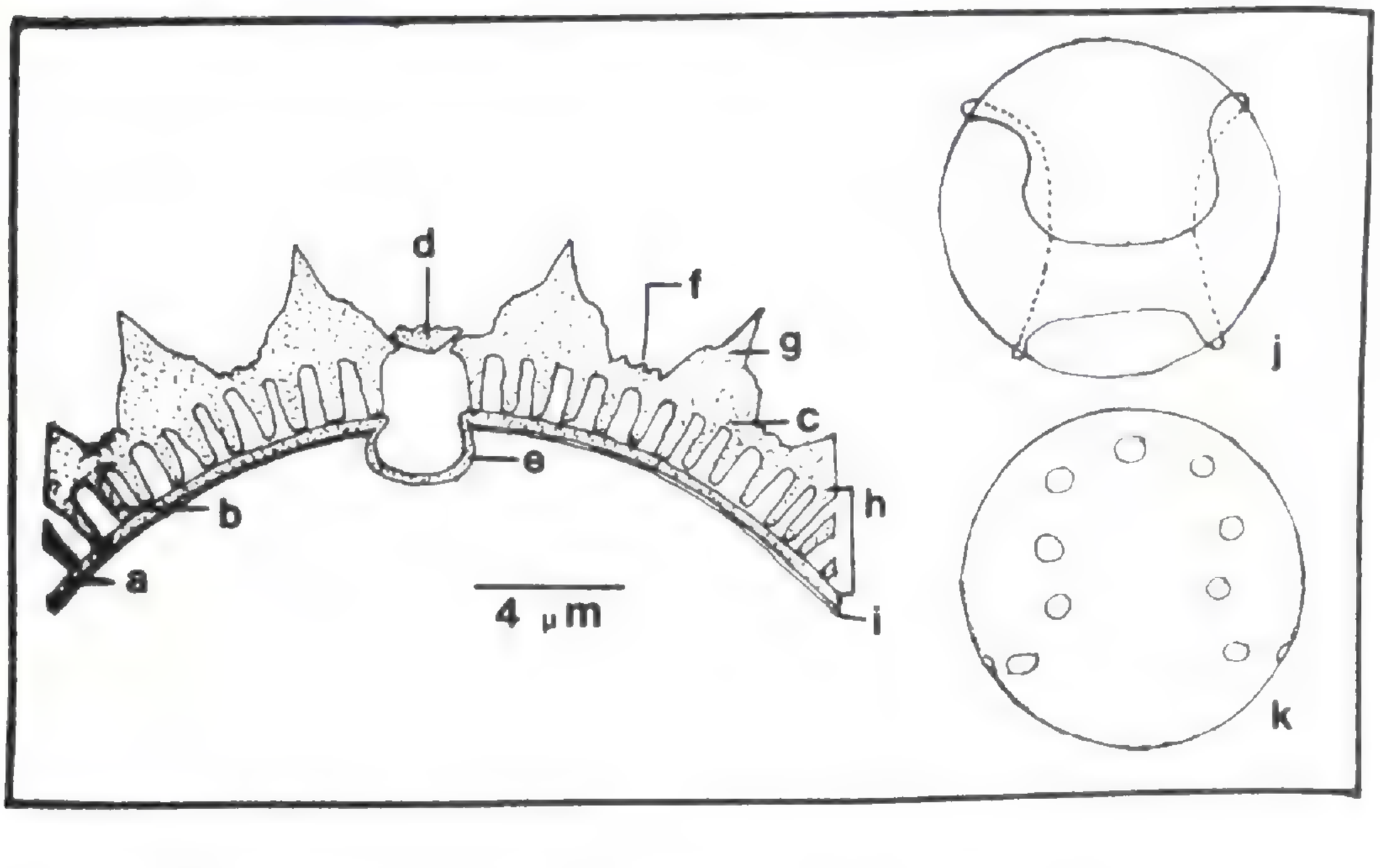


Figure 12. Pollen morphology in *Malvastrum*. a. Endexine. b. Ektexine columella. c. Tectum. d. Operculum. e. Apertural annulus. f. Verrucae. g. Spine (echina). h. Ektexine. i. Intine. j-k. Two views of most frequent aperture pattern—schematic (apertures not indicated in j; from Tressens, 1974).

M. hispidum all have glabrous staminal columns while those of the remaining taxa have at least a few hairs.

Anther number varies considerably both within and between taxa. The lowest number of anthers encountered is 5–6(7) in *M. spiciflorum*, followed by 8–13 (16) in *M. hispidum*. In each of these autogamous species the number is thought to be reduced from the usual number of 16–50 encountered in the majority (18) of the taxa. The highest number encountered is in the entomophilous *M. grandiflorum* with 108–111 stamens per flower. Stamen number tends to correlate with the type of pollination-system encountered, as do petal size and petal orientation.

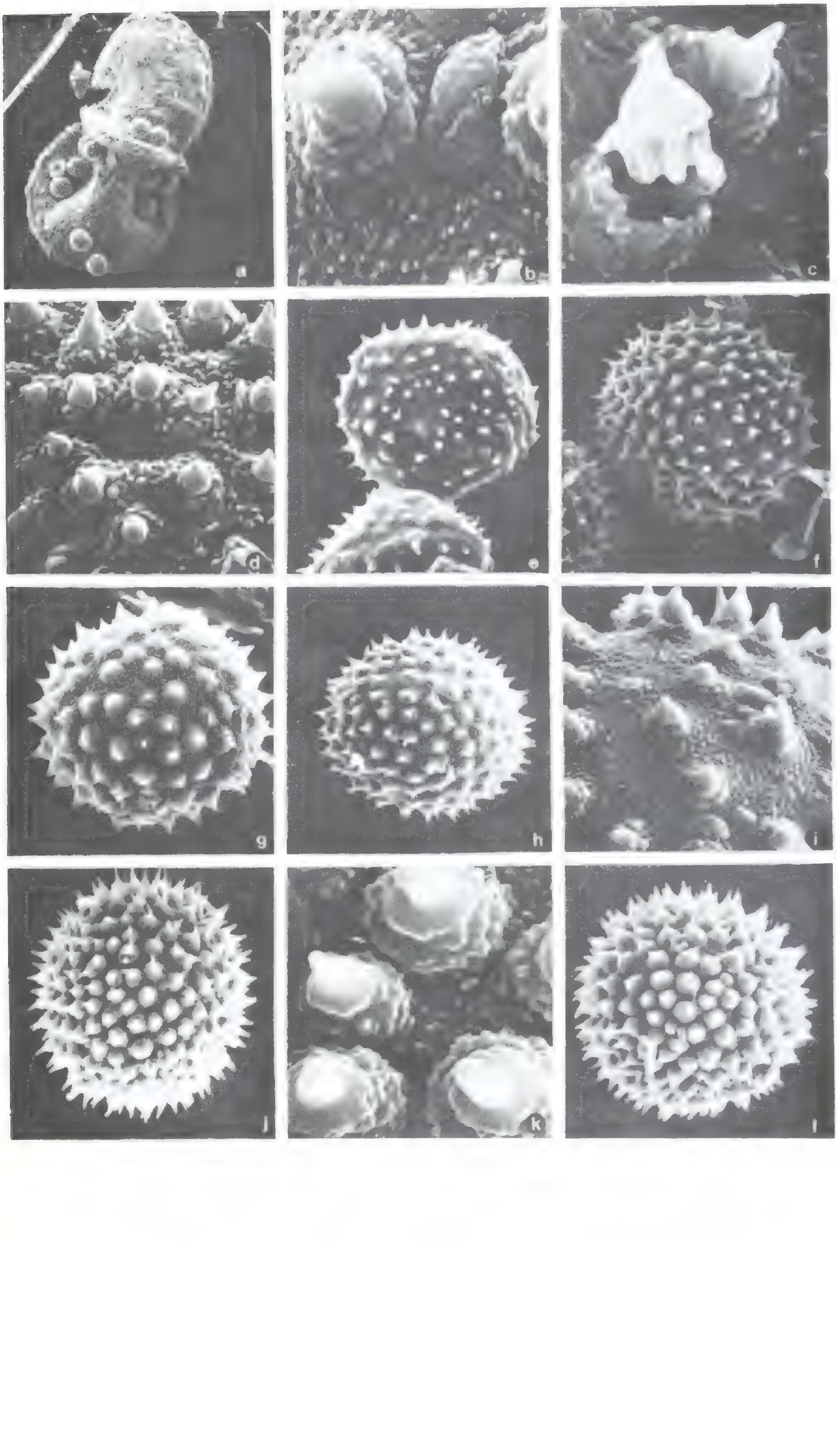
Pollen

The pollen produced by species of *Malvastrum* is spheroidal to slightly oblate, echinate, operculate, and panporate as in most other genera of the Malvaceae (Fig. 12–14). The grains vary in diameter from a minimum of 36 μm in *M. spiciflorum* to a maximum of 108 μm in *M. aurantiacum* (Fig. 13b, h & i), *M. coromandelianum* subsp. *coromandelianum* (Fig. 13j–k), and *M. grandiflorum*. The

average is 60–90 μm. The tectum is supported by a series of evenly-spaced columellae (Fig. 12b, Fig. 13c). The number of apertures varies from a minimum of 4–5 in *M. spiciflorum* to a maximum of about 35 in *M. grandiflorum*, with an average of 6–15 in the genus. The spines or echinae are rather short for the family, ranging from 2.3–3.8 μm in *M. spiciflorum* to a maximum of 10 μm in *M. aurantiacum*, averaging 4–7 μm in length. The apertures are usually arranged in a pattern resembling, in three dimensions, the seam of a tennis-ball or baseball and in two dimensions resembling a wide dumbbell (Fig. 12j–k, 14b). This pattern is most conspicuous in acetolyzed grains of *M. americanum, M. aurantiacum* (Fig. 13h), *M. coromandelianum*, and *M. hispidum* (Fig. 14b) but is obscure if the opercula are in place.

My measurements of pollen-diameter were consistently greater than those of Tressens (1974) who presented an excellent review of pollen in the genera *Malvastrum* and *Acaulimalva*. The difference was 4%–20% depending on the species. I feel that this was due to my preliminary KOH treatment which occasionally expands the grain. In addition, my measurements were taken from acetolyzed spores temporarily mounted in 70% alcohol, while Tressens recorded her diameters from specimens mounted in glycerine gelatin. However, other observations such as spine-length and aperture-number as well as relative size correspond well with Tressen's review, as well as measurements given by Hashmi (1970).

Figure 13. *Malvastrum* pollen I. a. Dehisced anther with several grains, *M. americanum (Parks & Cory 20661)*. b. Operculate aperture and ornamentation, *M.aurantiacum (Johnson 952)*. c. Spine structure showing columellae, *M. americanum (Parks & Cory 20661)*. d. Open aperture and ornamentation, *M. interruptum (Krapovickas et al. 18808)*. e. Immature surface ornamentation, *M. amblyphyllum (Krapovickas et al. 19127)*. f. Mature grain, *M. amblyphyllum (Krapovickas et al. 18558)*. g. Mature grain, *M. americanum (Parks & Cory 2066)*. h. Mature grain, *M. aurantiacum (Johnson 952)*. i. Ornamentation, *M. aurantiacum (Johnson 952)*. j. Mature grain, *M. coromandelianum* subsp. *coromandelianum. (Flores-Crespo 96)*. k. Ornamentation, *M. coromandelianum* subsp. *coromandelianum (Cory 36085)*. l. Mature grain, *M. coromandelianum* subsp. *fryxellii (Anderson et al. 9096)*. (a. 92×;b, d. 3960×; c. 5280×; e,f,j,l. 660×; g. 925×; h. 460×; i. 1320×; k. 4950×; magnifications calculated from instrument readings).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Gynoecium

The features of the gynoecium included in this review are the styles, stigmas, carpels, columella and carpocrater, and the ovules. Features of the gynoecium have been of great significance in delineating not only genera but also tribes in the Malvaceae.

In *Malvastrum* as in all other Malveae the single style branches above the ovary. In this genus the style is always glabrous. The branching in *Malvastrum* occurs at about 1/2 to 2/3 the distance above the apex of the columella and the number of branches equals the number of carpels. The style branches are erect or recurved. While in *M. grandiflorum* the branches remain erect even as the flower wilts, in most other taxa the branches recurve before, during, or after anthesis. This orientation, as discussed earlier, is very important to the breeding system as it can control outcrossing or self-pollination. The style or carpel number varies from a minimum of 5–6 in *M. hispidum* to a maximum of 18 in some individuals of *M. americanum* and *M. grandiflorum*. The unbranched portion of the style varies in length from 1.5–2.1 mm in *M. hispidum* and *M. spiciflorum* to a maximum of 12 mm in *M. grandiflorum*, and the branches vary in length from 0.5–0.8 mm in the former two to 7 mm in the latter. The styles may equal the stamens in height or exceed them by up to 5 mm.

While the capitate stigmas were among the first structures used to distinguish *Malvastrum* from other genera in the Malveae and from *Malva* in particular, when all of the taxa are examined not all of the stigmas are capitate (in the sense of being expanded at the terminus). In fact, in *M. chillagoense* the stigmas are smaller in diameter than the style branches. In *M. bicuspidatum* subsp. *campanulatum* the stigmas are subequal to the styles in diameter. Nevertheless, the stigmas are always terminal, never decurrent even slightly, and are mostly capitate with a subhemispherical to spherical shape and a

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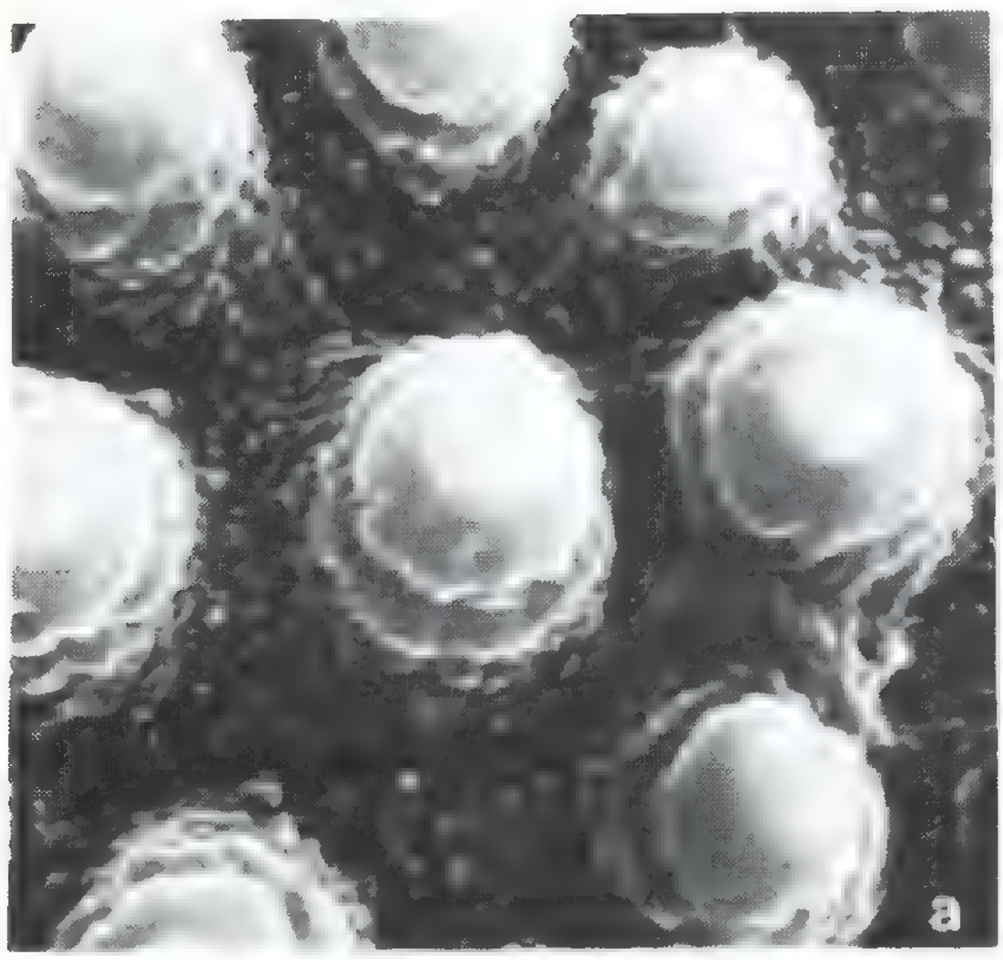
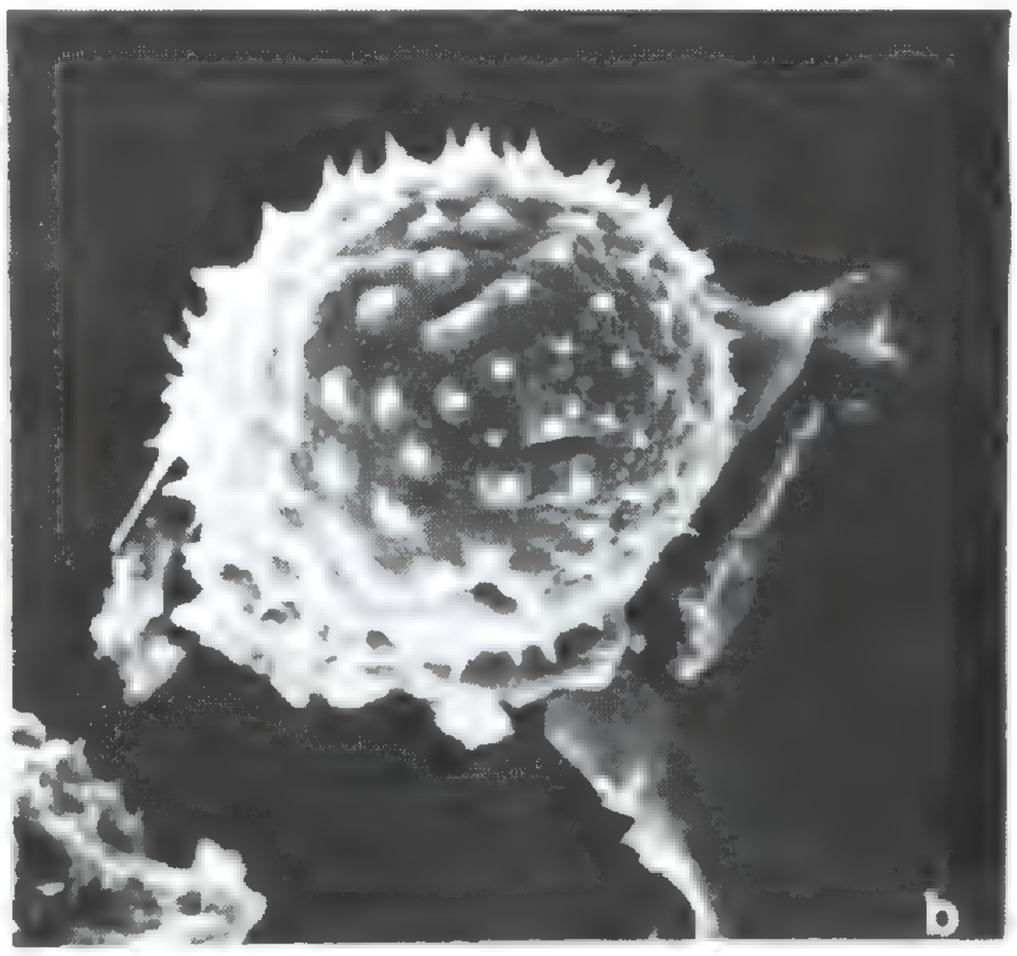
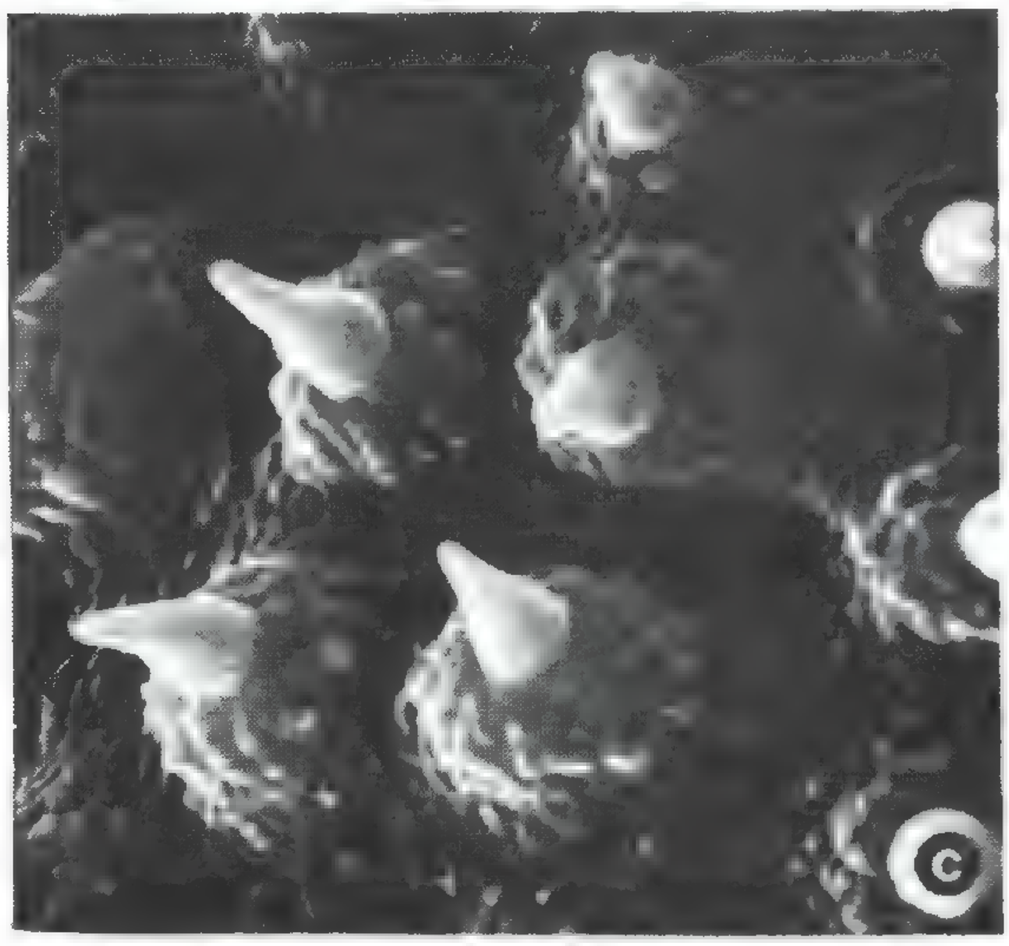
Figure 14. *Malvastrum* pollen II. a. Ornamentation, *M. coromandelianum* subsp. *fryxelli (Anderson et al. 9096).* b. Mature grain, some fungal damage, *M. hispidum (Bates 2705).* c. Ornamentation, *M. hispidum (Bates 2705).* d. Mature grain, *M. interruptum (Krapovickas et al. 18808).* e. Ornamentation, *M. interruptum (Krapovickas et al. 18808).* f. Mature grain, *M. scoparioides (*López & Sagastegui 7672); (a. 3300×; b-d. 660×; c. 3960×; e. 1980×; f. 725×; magnifications calculated from instrument readings).


a


b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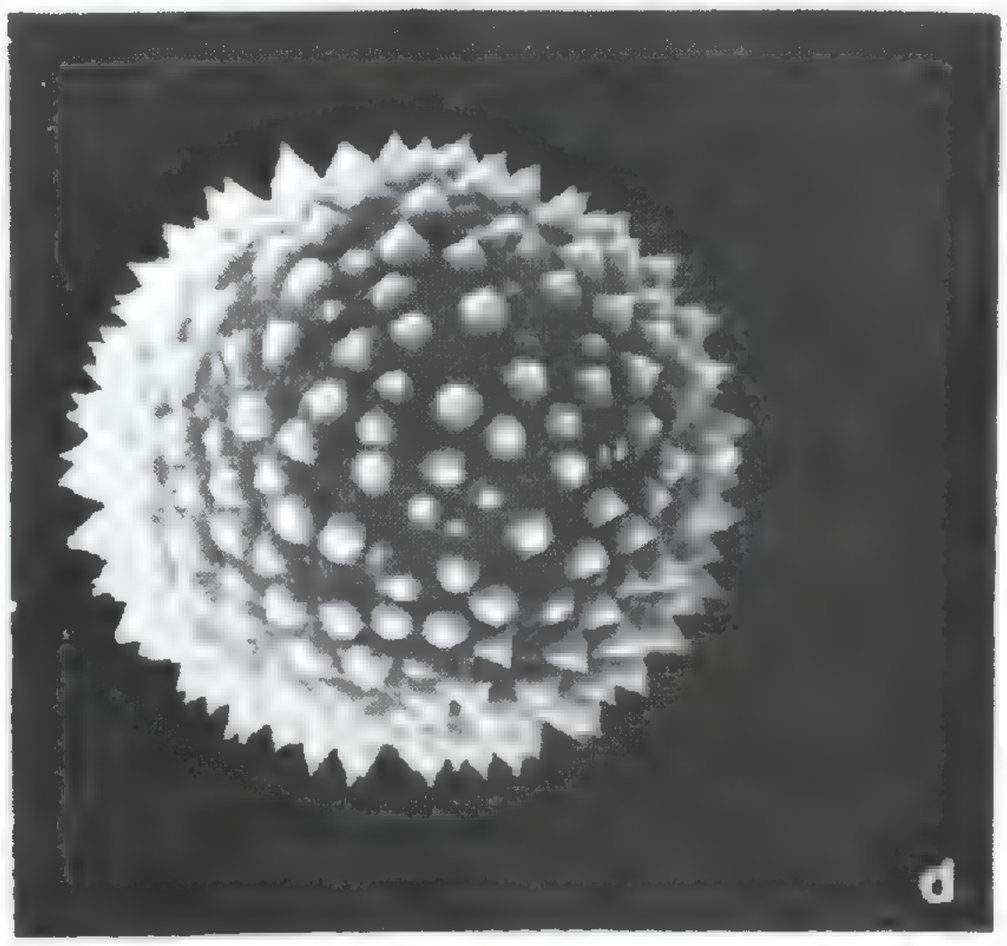
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e

f

papillose surface. The pollen-grain becomes rather firmly situated as its spines loosely interlock with the papillae. Usually only 1–4 grains can attach to a single stigma due to their size.

The carpels are loosely coherent or contiguous with one another but are adnate to the central columella, a structure that in position closely resembles the placental axis of capsular fruits in the Malvaceae. The number of carpels, 5 6 to 18, varies between and within species, but the range in variation can aid in species determination. As an example of intraspecies variation, the number may vary from 9 to 18 in *Malvastrum americanum*. Usually the number varies a great deal less than that. The carpel wall in *M. coromandelianum* has 4 layers of tissue (Fig. 15): an obscure epidermis, an exocarp of large irregular parenchyma cells, a mesocarp region of small sclerenchyma cells that is greatly thickened to form the cusps, and a single-celled endocarp of small firm cells that lines the locule. From the epidermis arise the translucent, firm, centrally (proximally) directed simple to multiradiate stellate hairs of the apical surface.

The columella is a generally persistent cylindrical, clavate, or peltate structure at the center of the calyx to which the carpels and style are attached. It is usually expanded above its base before fruit maturity and so produces a medial notch on the proximal margin of each mericarp corresponding to this expanded zone. It seems evident that its shape and dimensions can be of limited diagnostic use. For example, *M. bicuspidatum* subsp. *bicuspidatum* has a flared columella with a narrow base which contrasts with the turbinate columella of *M. bicuspidatum* subsp. *campanulatum*. This results in the very deep proximal notch in mericarps of the former and shallow notches in those of the latter. Variation in the columella does not seem to be of great diagnostic value above the species level in *Malvastrum* and varies to an extent within a single plant as it dries in fruit.

Associated with the columella and perhaps a basal outgrowth of it is a thin disc of tissue that is cartilaginous to chartaceous in the center and membranous or hyaline marginally. This is the carpocrater, a term proposed by Hochreutiner (1920) and applied by him to the structure as found in the genus *Cristaria*. The carpocrater in *Malvastrum* is far less developed than in *Cristaria*. It varies in diameter among the taxa but does not seem to be of great diagnostic value in *Malvastrum*. The carpels are completely free of the carpocrater but are subtended by it.

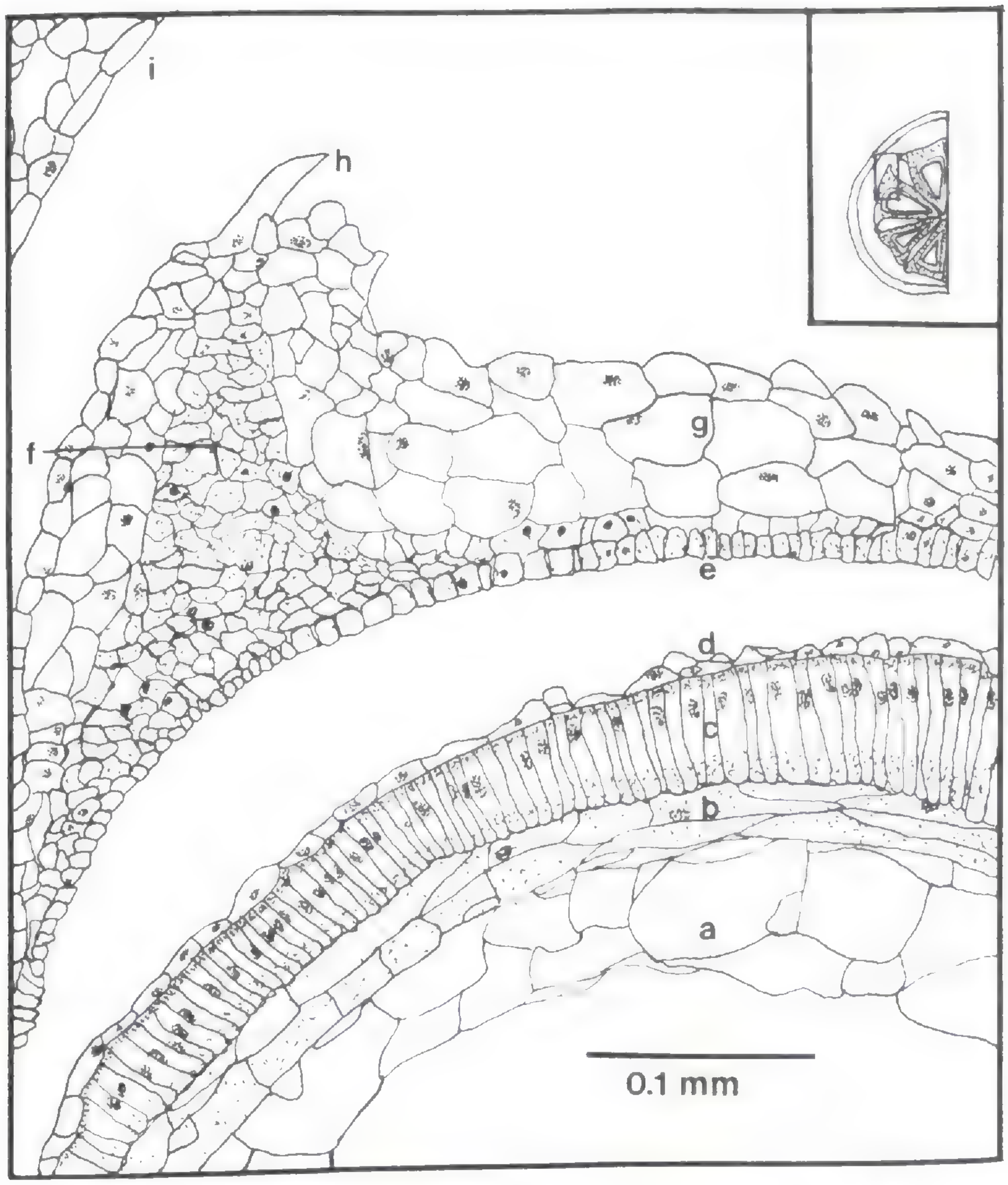


Figure 15. Seed and fruit tissues, *Malvastrum coromandelianum*. a. Endosperm. b. Inner integument. c. Outer integument. d. Epidermis of outer integument. e. Endocarp. f. Sclerenchymal support tissue for mericarp cusp (mesocarp) g. Exocarp h. Trichome. I. Calyx. Inset: portion of fruit enlarged. Camera lucida, (*Hill 5112*).

The ovules in *Malvastrum* are always solitary and ascending in each carpel. Each is attached to the axile (proximal) placenta of the columella by a minute funiculus that is located immediately below the medial ovule-notch. The micropyle is present below the funiculus, and the young embryo begins its development in this lower region. As the embryo develops, the radicle is inferior. The endosperm is consumed by the embryo, but tissues are not well differentiated in the dormant seed.

Fruit

The mature ovary of *Malvastrum* is a complex oblate to discoid schizocarp. It consists of the mature carpels or mericarps associated with the central columella and carpocrater, and is enclosed by the accrescent persistent calyx. In most cases the dried corolla persists for a time, adhering to the withered style at the center of the fruit. The calyx itself may by means of its lobes enclose the fruit and prevent rapid dispersal or may expose the fruit allowing rapid dissemination. The pedicel, calyx, and columella normally do not abscise from the inflorescence axis.

The individual mericarps are either schizocarpic achenes or schizocarpic follicles depending on whether they are indehiscent or dehiscent, respectively. When the mericarps separate from the columella along the proximal surface, a small portion of the wall remains attached and a narrow opening in the region of the hilum results. In this sense, the seed is no longer attached to the pericarp. The opening is too small to allow the seed to escape.

The mericarp is the single most important structure used to determine taxa in *Malvastrum*. This is due to several facts: 1) the mericarps scarcely vary in morphology within a given taxon and so have been traditionally used to distinguish taxa in the tribe Malveae, 2) the mericarp often exhibits important specializations or structures suggesting the relationships of taxa, 3) the mericarps are usually present in both living individuals and herbarium specimens, and 4) the other structural features of the plant, both vegetative and reproductive, are often too variable to allow a definitive determination. For these reasons keys to the taxa are generally dependent upon characteristics of the mericarps. While often small, the important characters are visible with a hand lens. In shape the mericarp simulates a wedge cut from an oblate wheel of cheese. There are three surfaces: two lateral surfaces and a continuous apical-distal-basal surface. There is a single nearly straight proximal margin and two curved lateral margins. I feel that in the Malveae the terms proximal and distal referring to the relationship of the carpel and the columella are more precise and easily understood than the terms dorsal and ventral. The mericarps are conspicuously notched in direct relation to the amount of expansion in the upper portion of the columella. In mature fruits the columella has shrunken and drawn away from the notch, facilitating mericarp separation.

The size of the mericarp is of diagnostic value, but mostly in the case of the extremes. The height including ornamentation varies from a minimum of 1.0–1.5 mm in *Malvastrum spiciflorum* to a maximum of 6 mm in *M. aurantiacum*, the length varies from a minimum of 1.0 1.5 mm in *M. chillagoense* and *M. spiciflorum* to 5–6 mm in *M. aurantiacum*, and the width varies from 0.8 mm in *M. americanum* and *M. interruptum* to 2.0 mm in *M. amblyphyllum* and *M. grandiflorum*.

The pericarp is usually pubescent on the external apical surface, the apical and distal margins of the lateral surfaces, and, to a lesser degree, on the apical half of the distal surface. A few sparse hairs may occur in other regions. The hairs vary in type and density and are of diagnostic value. One taxon (*Malvastrum bicuspidatum* subsp. *tumidum* var. *glabrum*) has glabrous mericarps. The pericarp is usually green until it reaches maturity and dries to tan or brown. The mericarps of *M. aurantiacum*, *M. bicuspidatum*, and perhaps a few others not cultivated in this study become rose or raspberry-red and are very conspicuous in later immature stages, but at full maturity fade to tan or brown.

The pericarp is often ornamented with one or more mucros or cusps. This ornamentation is completely lacking on the mericarps of *Malvastrum chillagoense*, *M. hispidum*, and some populations of *M. americanum*. A minute single proximal apical mucro less than 0.1 mm in length is present on the mericarps of *M. interruptum*, *M. spiciflorum*, and the remaining populations of *M. americanum*. All of the other taxa have two or three conspicuous to obscure cusps or mucros. In the sections *Amblyphyllum* and *Tomentosum* there is a single proximal-apical mucro or small cusp 0.1–1.0 mm long and two distal-apical often conspicuous cusps 0.5–2.0 mm long on the pericarp. The cusp is often vertically dehiscent in the section *Tomentosum*. In the section *Malvastrum* the very conspicuous apical cusp, 1.0–2.3 mm long, is set nearly midway between the proximal and distal margins giving it a different aspect; the distal-apical cusps are also present but are generally smaller (0.2–1.1 mm long). In *M. aurantiacum* the distal cusps are flattened contiguous apparently non-functional vestigial structures. The cusps are often beset with conspicuous bristle-hairs up to 1.0 mm long that may aid in dispersal by increasing the tendency to become "hooked" on fur, feathers, or clothing.

In addition to the cusps, the mericarps of *M. amblyphyllum* and *M. grandiflorum* have prolonged, briefly winged distal-lateral margins that are thin and translucent between their supporting ribs. The wings are so short (up to 0.5 mm long) that their value as a dispersal aid is obscure.

The thickness of the pericarp and its texture can also be diagnostic. In *Malvastrum hispidum, M. interruptum,* and *M. spiciflorum* the lateral faces are thin and nearly translucent. In *M. bicuspidatum* subsp. *tumidum* and subsp. *oaxacanum* the pericarp is shiny and leathery or chitinous and of moderate thickness. The remaining taxa have firm dull soft-woody pericarps that often have radial lateral supportive ribs. Those taxa with the most conspicuous cusps also usually have the thickest pericarps and the best rib-development. This probably gives added strength to mericarps adapted to long-distance transport.

The degree of dehiscence of the pericarp is variable within the genus. While *Malvastrum* was formerly considered to have only indehiscent or slightly dehiscent mericarps (Kearney, 1955), one taxon with completely dehiscent mericarps (*M. hispidum*) is now included in the genus. The mericarps of *M. americanum* and *M. corchorifolium* tardily split along the medial suture of the basal region to release the seed. The mericarps of the remaining taxa do not split, but the mericarps of several taxa, including *M. americanum, M. corchorifolium, M. coromandelianum, M. scoparioides,* and *M. tomentosum,* are unsealed at the proximal apical margin above the notch at maturity. In nearly every taxon, including those with indehiscent pericarps, a medial line or suture is present along the apical-distal-basal surface suggesting a connection with ancestral forms with loculicidally dehiscent mericarps as in *M. hispidum.*

The presence of absence of an endoglossum is of diagnostic value at the specific and subspecific level in *Malvastrum* although this structure is often small. When present, the endoglossum is found slightly distal to the proximal-apical margin on the internal apical surface. It is a small intrusive tissue that incompletely divides the lustrous internal chamber into a large seed bearing chamber and a small empty proximal-apical 'chamber.' The proximal margin of this 'chamber' may or may not be sealed, as described above. Those taxa with an endoglossum or endoglossum remnant include *M. bicuspidatum* subsp. *oaxacanum, M. corchorifolium, M. scopari-*

oides, M. tomentosum (both subspecies), and most populations of *M. americanum.* The remaining taxa lack this structure.

Seeds

Malvastrum seeds are basically reniform and have a very firm, three-layered seed coat that is completely glabrous. The outer layer of the seed coat (Fig. 15d) consists of a fragile external tissue that may produce a thin wax layer giving the seed a glaucous appearance. This coat is often absent or worn away after the seed is shed. The second layer is composed of densely-packed, radially elongated, heavily sclerified cells that are reduced in size in the regions of the notch and hilum (Fig. 15c). The third layer is composed of thin, non-sclerified tissues (Fig. 15b). The thick seed coat contributes to the durability and longevity of the seed. The seed retains a soft proximal-basal flap of placental or hilum tissue, which is often lost in age through abrasion. The color of the seed coat varies from gray to chestnut-brown or black.

Seed shape is determined by the shape of the enclosing pericarp to which the seed conforms when it is immature. The seed shrinks slightly as the seed coat hardens (shrinkage is most pronounced in *M. aurantiacum*). In some taxa of the section *Tomentosum* the seed has a medial distal-apical sulcus that conforms to the firm indented pericarp and enlarged cusps in that region, as in *M. bicuspidatum* (subsp. *bicuspidatum,* subsp. *campanulatum,* and subsp. *tumidum*), *M. guatemalense,* and *M. tomentosum* subsp. *tomentosum.* The seed of *M. aurantiacum* bulges in this same region conforming with the chamber expansion in that cusp area. Seeds from unusual populations of *M. americanum* var. *americanum* from northern Queensland, Australia, with apically prolonged mericarps have correspondingly narrow elongated seeds. In nearly all of the species the reniform seed shape is modified by the pericarp so that the portion below the notch is narrower and attenuated compared to the broader apical half.

Seed size varies in radial length from a minimum of 1.0 mm in *M. spiciflorum* to a maximum 2.5 mm in length in *M. aurantiacum* and *M. hispidum;* the height varies from 1.0 mm in *M. spiciflorum* to 2.5–3.0 mm in *M. aurantiacum;* and the width varies from 0.6–0.7 mm in *M. spiciflorum* to 1.3 1.5 mm in *M. aurantiacum* and *M. hispidum.*

Chromosome numbers

Chromosome numbers for members of the genus *Malvastrum* are summarized in Table 3, including counts obtained during the course of this study. I found that mitotic counts could be most readily obtained from apical and root meristems of seedlings at the early cotyledon-stage as the tissues were more difficult to hydrolyze at later stages. The seedlings were first pretreated in a saturated aqueous solution of monobromonaphthalene for 4 hours and then were fixed in a 3:1 ethanol: glacial acetic acid solution overnight. Next the seedlings were hydrolyzed in 1 N HCl for 30 minutes at 60° C, and the shoot and root meristems were placed in Feulgen staining solution for another 30 minutes. The meristems were then isolated and squashed in a drop of aceto-carmine solution and examined. Flower buds for meiotic counts were also pretreated as above, but after being fixed, the anthers were macerated in a drop of aceto-carmine, heated briefly over an alcohol flame, squashed and examined. My results were consistent with those of previous investigators. Selected preparations are illustrated in Figs. 16 and 17.

The base number found in *Malvastrum* is $x = 6$. Of the 22 taxa of *Malvastrum,* counts are known for all but six (i.e., *M. americanum* var. *stellatum, M. chillagoense, M. guatemalense, M. bicuspidatum* subsp. *tumidum, M. bicuspidatum* subsp. *tumidum* var. *glabrum,* and *M. tomentosum* var. *pautense*). There is only a single known diploid, *M. spiciflorum, 2n* = 12. Among the remaining 15 taxa whose chromosomes have been examined, 10 are tetraploids with counts of $n = 12$ or $2n = 24$, and three (*M. aurantiacum, M. hispidum,* and *M. interruptum*) are hexaploids with reported counts of $n = 18$ or $2n = 36$. *Malvastrum corchorifolium* is an octoploid with counts of $n = 24$ or $2n = 48$. *Malvastrum scoparioides* may also be an octoploid with the single tentative count $2n$ = ca. 48. Aneuploids have not been recorded for the genus.

The chromosomes are mostly acrocentric but (as in *M. americanum, M. corchorifolium,* and *M. coromandelianum*) 1 or 2 pairs are metacentric. In addition, usually 1 to 3 pairs have satellites (Fig. 16 d–d′ and 17 a–a′). An idiogram of *M. coromandelianum* (as *M. tricuspidatum*) has been prepared by Hazra and Sharma (1971).

Table 3. **Chromosome numbers in Malvastrum.** References are to previous counts, vouchers cited refer to new counts.

Taxon	Count	Reference or Voucher
M. amblyphyllum	$2n = 24$	Krapovickas, 1954b; *Krapovickas 18558* (cult.)[1]
M. americanum	$n = 12$, $2n = 24$	Skovsted, 1935, 1941; Krapovickas, 1951, 1954b; Bates, 1976; *Hill 6051*[2,3]; *Hill 7640*[3]; *Hill 6054*[3]; *Molina 27315* (cult.)[1]; *Percival s.n.* (cult.)[1]; *Seymour 2362* (cult.)[1,4]; *Ventura 2622* (cult.)[1]; *Williams et al. 23805* (cult)[1,4]; *Croat 9705* (cult.)[2]
M. aurantiacum	$n = 18$, $2n = 36$	Bates & Blanchard, 1970; *Hill 6430* (cult.)[1]; *Hill 5878*[3]
M. bicuspidatum subsp. *bicuspidatum*	$n = 12$, $2n = 24$	Bates, 1976; *Bye 6940* (cult.)[3]; *Gentry 14522* (cult.)[3]; *Lehto et al. 19487* (cult.)[1,3,4]
M. bicuspidatum subsp. *campanulatum*	$n = 12$, $2n = 24$	Krapovickas, 1969; Bates, 1976
M. *bicuspidatum* subsp. *oaxacanum*	$2n = 24$	*Krapovickas 23596* (cult.)[1]
M. corchorifolium	$n = 24$, $2n = 48$	Krapovickas, 1967; Newton & Kisseadoo, 1978; *Contreras 5588* (cult.)[3]; *Correll 43854* (cult.)[1]; *Correll 45520* (cult.)[1]; *D'Arcy 394* (cult.)[1]; *Fryxell 2861* (in part, cult.)[4]; *Lakela 27892* (cult.)[1]; *Molina 27248* (cult.)[1]; *Seymour 6129* (cult.)[1]; *Standley 25780* (cult.)[1]
M. coromandelianum subsp. *coromandelianum*	$n = 12$, $2n = 24$	Skovsted, 1935, 1941; Krapovickas, 1951, 1954b; Roy & Sinha, 1961; Bates, 1967b; Hazra & Sharma, 1971; Bir & Sidhu, 1975; Newton & Kisseadoo, 1978; *Fryxell, s.n.* (cult.)[1]; *Hall s.n.* (cult.)[1,4]; *Hill 4465*[1]; Hill 4579 (cult.)[1]; *Hill 5806*[2]; *Hill 5889*[3]; *Hill 6061*[3]; *Morel 8095* (cult.)[4]

Table 3. **Chromosome numbers in Malvastrum.** References are to previous counts,

Taxon	Count	Reference or Voucher
M. coromandelianum subsp. *capitato-spicatum*	n =12, $2n$ = 24	Krapovickas, 1949; Bates 1967b
M. coromandelianum subsp. *fryxellii*	$2n$ = 24	*Anderson et al. 9096* (cult.)[1,4]
M. grandiflorum	n = 12	Krapovickas, 1974b
M. hispidum	n = 18	Bates, 1967a
M. interruptum	n = 18, $2n$ = 36	Krapovickas, 1954b; *Gutiérrez 357* (cult.)[1]; *Krapovickas 22103* (cult.)[2,3]
M. scoparioides	$2n$ = ca. 48	*López & Sagastegui 8020* (cult.)[1]
M. spiciflorum	$2n$ = 12	Krapovickas, 1954b
M. tomentosum	n = 12, $2n$ = 24	Skovsted, 1935; Krapovickas, 1967, 1969. *Iltis 1591* (cult.)[1,2,3,4]; *Stork 8973*[2,3]

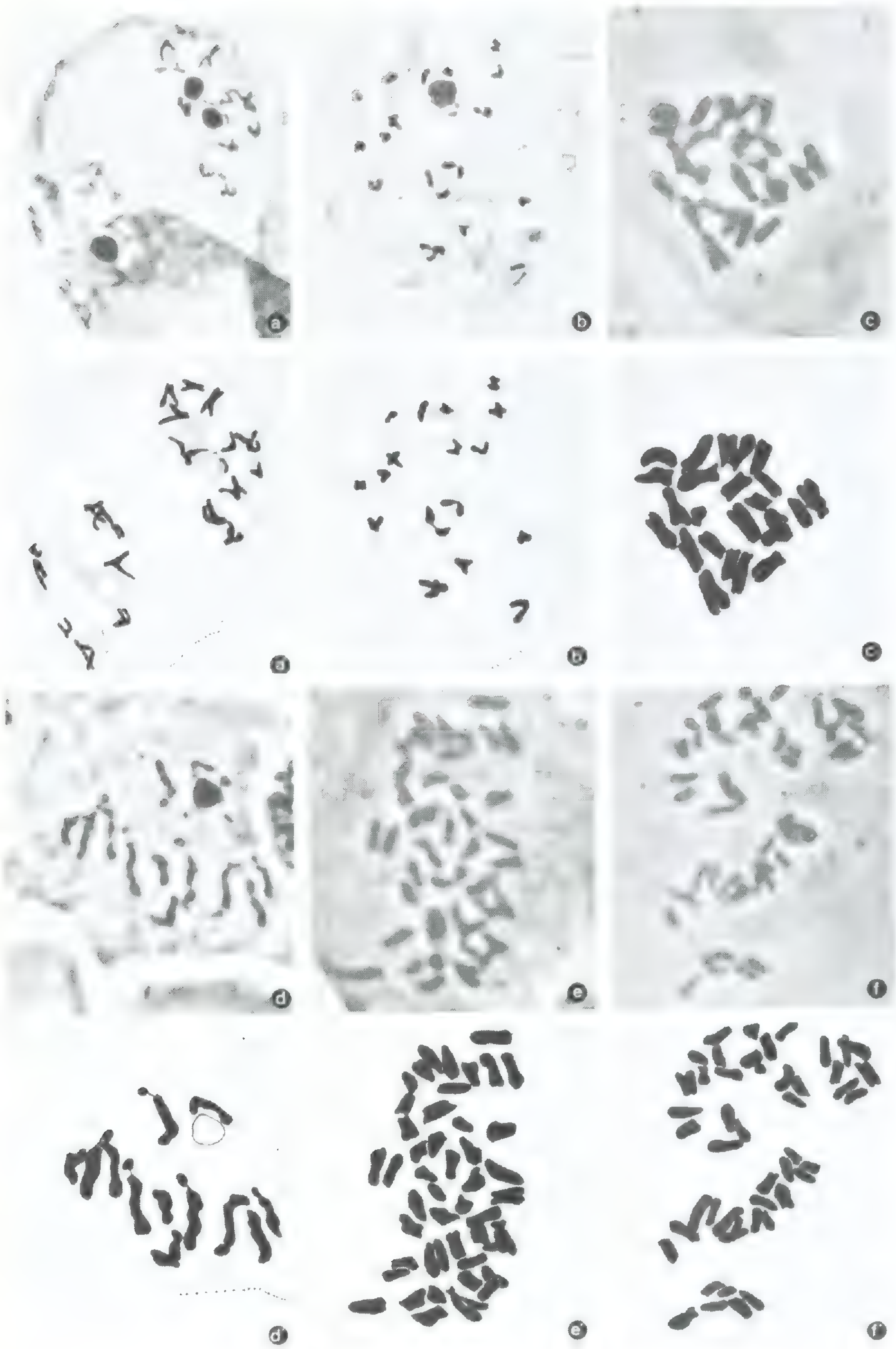
[1]root tip
[2]pmc
[3]yng. pollen
[4]shoot apex

PHYLOGENY

Infrageneric relationships

While the phyletic accuracy of all of the approaches to cladistics can be debated (see Funk & Stuessy, 1978), in order to demonstrate graphically one possible scheme of relationships within *Malvastrum* I have prepared a cladistic diagram (Fig. 18) using the Wagner Groundplan/Divergence method (Wagner, 1961). Phenotypic expressions for 60 characters were recorded for each of the taxa (see Appendix 11) and divergence-values based on an hypothetical

Figure 16. *Malvastrum* chromosomes. I. a-a′. *M. americanum*, $2n$ = 24, pollen mother cell, anaphase I (cult. *Croat 9705*). b-b′. *M. aurantiacum*, n = 18, immature pollen, prophase II (*Hill 5878*). c-c′. *M. bicuspidatum*, $2n$ = 24, root tip, metaphase (cult. *Lehto et al. 19487*). d-d′. *M. bicuspidatum*, n = 12, immature pollen, telophase II (cult. *Lehto et al. 19847*). e-e′. *M. corchorifolium*, $2n$ = 48, root tip, metaphase (cult. *D'Arcy 394*). f-f′. *M. corchorifolium*, $2n$ = 48, root tip, metaphase (cult. *Lakela 27892*). All 696×.


a
b
c
d
e
f

ancestral state, designated as the origin, have been totaled for each taxon. Distances between the taxa have been determined by totaling the number of differences in their character states. These distance values, in combination with other characters such as geography and chromosome-number that are not included in the data matrix, have been used to determine the connections between taxa or with hypothetical taxonomic units (HTU's).

The scheme presented here is based upon *a priori* considerations concerning primitive and derived states within *Malvastrum* and the Malveae. In several cases the primitive character-state is considered to be not that which is most widespread in the genus but, instead, that from which other states are most probably derived. For example, even though only a single species, *M. hispidum*, has completely dehiscent mericarps (character 56) this is thought to be the ancestral state. While dehiscence could conceivably be a secondary development, it is not likely when all Malveae are considered. This follows from the fact that several rather unspecialized taxa have partially dehiscent mericarps and several related genera in the Malveae (e.g. *Tarasa, Malacothamnus,* and *Nototriche*) have completely dehiscent mericarps. In addition, dehiscence is characteristic of multi-seeded mericarps while indehiscence is characteristic of 1-seeded mericarps, which are derived.

The character-states for the flowers (characters 18–36) reflect the *a priori* assumption that the smaller, mostly autogamous flowers are derived from an earlier state involving moderate-sized entomophilous flowers. The flowers were probably reduced in size independently in the several taxa involved. A weakness in the distance matrix (Appendix II) results when all the small-flowered taxa are considered similar (such as *M. chillagoense* and *M. spiciflorum* which are actually considered to be only distantly related).

Several characters modified in one direction in the genus as a whole seem to have reversed in trend within individual sections of

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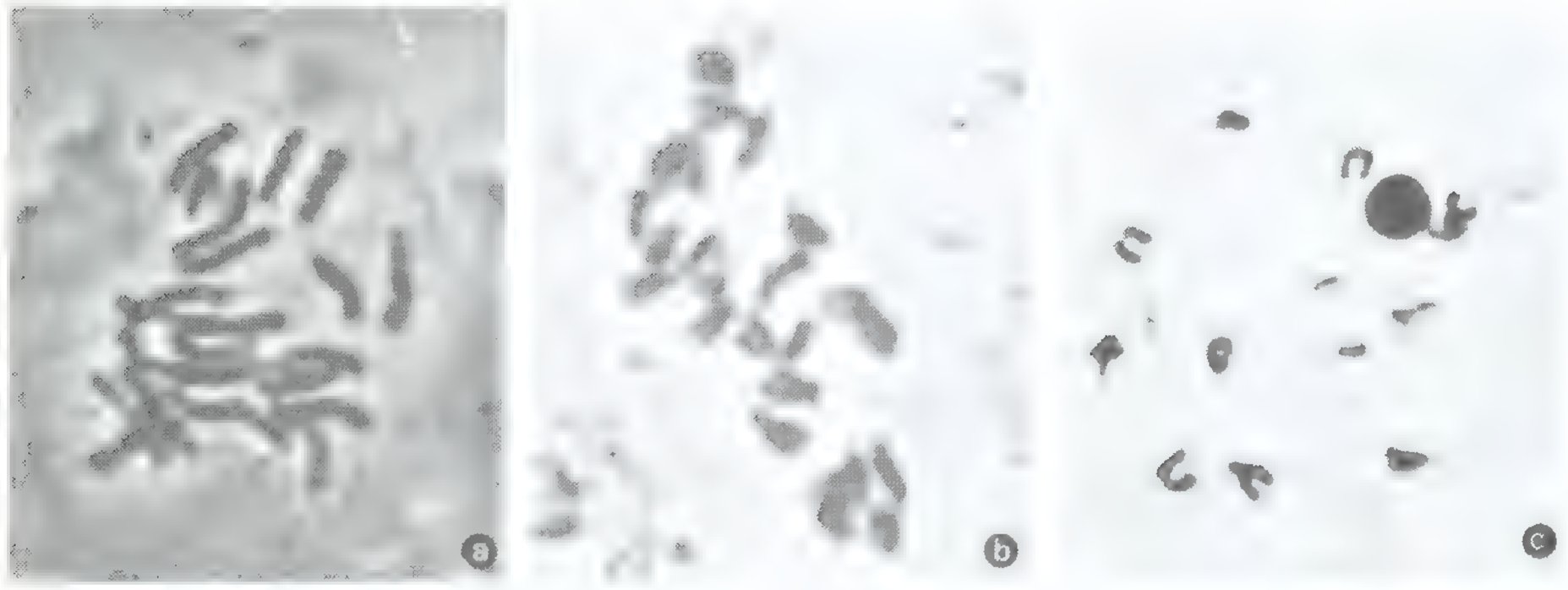
Figure 17. *Malvastrum* chromosomes II. a-a'. *M. coromandelianum*, $2n = 24$, root tip, metaphase (*Hall s.n.*, seeds only, Ghana). b-b'. *M. coromandelianum*, $2n = 24$, root tip, metaphase (cult. *Hill 4465*). c-c'. *M. coromandelianum*, $n = 12$, pollen mother cell, late prophase II (*Hill 5806*). d-d'. *M. interruptum*, $n = 18$, pollen mother cell, late prophase I (cult. *Krapovickas et al. 22103*). e-e'. *M. tomentosum*, $2n = 24$, root tip, metaphase (cult. *Iltis & Iltis 1591*). f-f'. *M. tomentosum*, $2n = 24$, pollen mother cell anaphase I (cult. *Iltis & Iltis 1591*). All 696×.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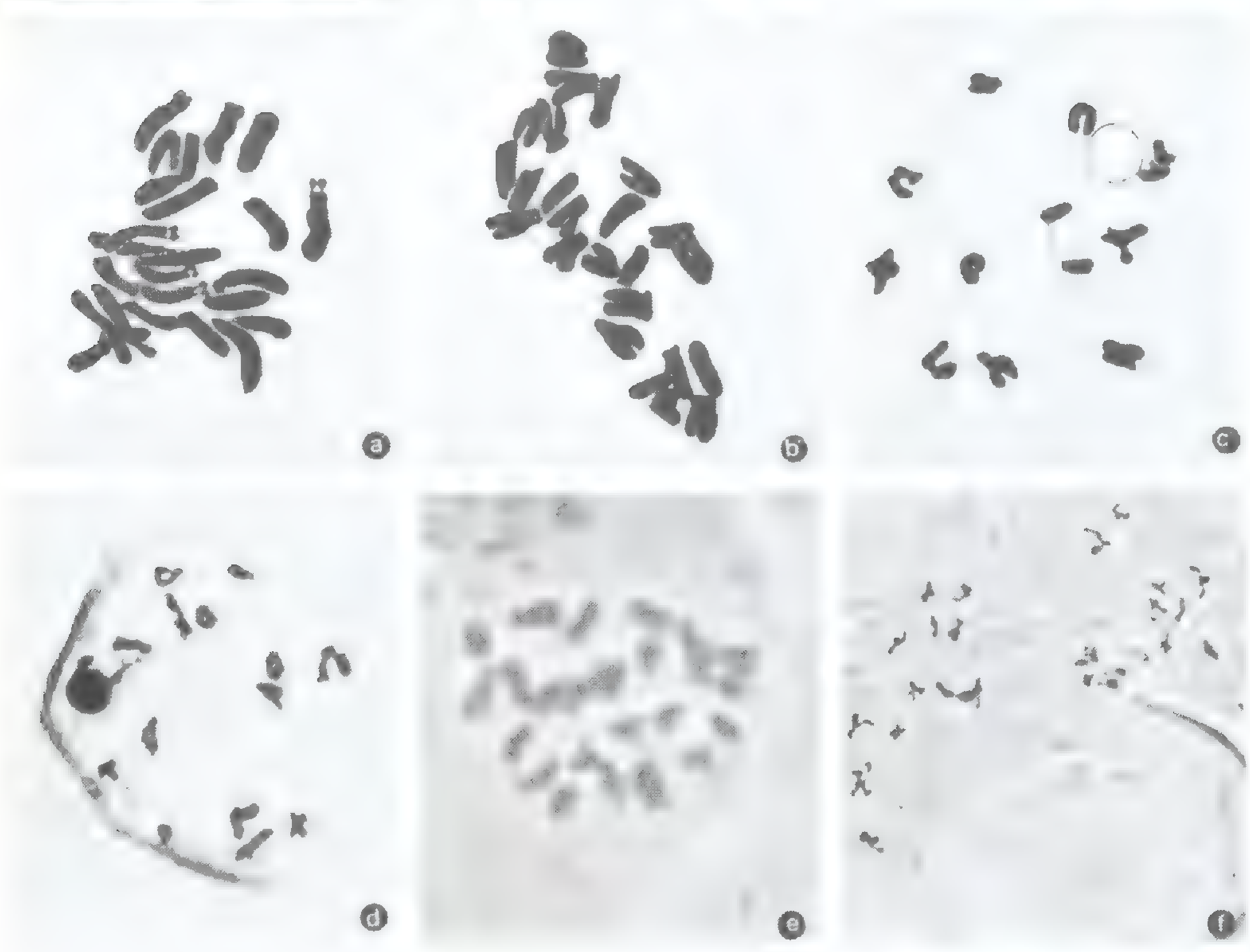
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the genus or to have taken several directions. In at least one case the character reversal cannot be readily indicated (e.g. character 16, some taxa may have solitary axillary flowers as a result of a neotenous reversal from that of a more complex inflorescence). In another case an attempt has been made to indicate a character reversal (e.g. character 49, cusp length, where the shorter cusps of several taxa are considered to be derived from the larger ones). Characters that have probably developed in several directions are indicated by intermediate values (e.g. vesture characters 3, 14, 15, 27 and 55, stamen number character 34, inflorescence character 16, and petal length character 28) with lower values assigned to the less specialized states. As a result of the problems inherent in this system the distance matrix must be considered together with independent trends in certain characters.

While the character states are useful to indicate relative specialization from an ancestral state, certain characters indicative of particular environmental situations are not considered to be especially useful in indicating true relationships. Characters such as duration (1), height (2), and leaf morphology (5 13) are not the best guides to relationships within *Malvastrum* and so have been given lesser importance in connecting taxa. Since these eleven characters are less than 20% of the total number they have affected the results to a lesser extent than have the majority of characters that seem to have phyletic value.

The data matrix presented in Appendix II allows the proposal of HTU's through which the extant taxa may be related. Characters that are primitive and shared within groups of taxa are used to propose a common connection at the shared level of divergence (the common ancestor). For example, all the members of the section *Tomentosum* share the same values for characters 1, 2, 4, 10, 11, 29, 30, 31, 33, 35, 36, 40, 47, 48, 56, and 58, the combination of which defines the HTU ancestor of the section.

One of the results of this numerical analysis has been the division of *Malvastrum* into seven sections. The first three sections (sect. *Sidopsis, Interruptum,* and *Americanum*) retain basically unornamented mericarps while the remaining four sections have ornamented mericarps.

The most divergent species, *M. hispidum,* is placed in the section *Sidopsis* (Fig. 18A).It was found to share a number of characters with members of section *Interruptum,* but differed from members of

tha section in nearly half of its characters. It seems to have been separated from the mainstream of *Malvastrum* evolution for a longer period than any other taxon based on its divergence value (differing from the ancestral state by 44 of the 60 characters) and its unusual disjunct occurrence in temperate North America. The completely dehiscent carpels, here viewed as the retention of a primitive character, have been used in the past to maintain the species as generically distinct from *Malvastrum*. The origin of *M. hispidum* remains obscure.

In contrast, section *Interruptum* (Fig. 18B) is one of the least divergent from the supposed ancestral state. The diploid *Malvastrum spiciflorum* retains a greater number (35) of presumed primitive characters than any other species with the exception of *M. americanum* (37) and would be placed even closer to the ancestral state were it not for its reduced flowers. *Malvastrum interruptum* has retained the larger flowers but is isolated from *M. spiciflorum* by its higher ploidy level. The two species share 37 characters of the 60 considered and also seem to have a similar ecology.

Members of the section *Americanum* (Fig. 18C), like those of section *Interruptum*, also retain many ancestral characters. This section poses an unresolved phytogeographic problem in that it is diverse not only in the New World but also in eastern Australia. *Malvastrum chillagoense*, thought to be derived from an early form of *M. americanum*, is seen to be more similar to other taxa according to the distance matrix (Appendix II) than to *M. americanum* but this probably reflects a simplification of characters during geographic isolation rather than any true relationship. Some populations of *M. americanum* var. *americanum* in northern Queensland, Australia show a trend of specializations similar to those of *M. chillagoense*. Vegetative and pollen characters further strengthen the affinity.

The section *Tomentosum*, composed of nine taxa in four species, shows the greatest coherence (Fig. 18D). Members of this section have been taxonomically and nomenclaturally confused for two centuries due to an incomplete understanding of their ranges, ecology, and morphology. The Central American members of the section seem to have differentiated in comparatively recent times since 60% of their examined characters are shared. As discussed previously, adaptive radiation may have occurred after an ancestral population was introduced into the region via the Central American

land-bridge. The populations then became discontinuous as climatic and geologic conditions changed. Because of a supposed early dependence on animal dispersal within the group, the taxa with long cusps and stronger pericarps are considered to be more primitive than those with smaller cusps and a leathery pericarp; this is the reversal of a trend found in the genus as a whole. Three taxa of the section remain in South America. Both *Malvastrum scoparioides* and *M. tomentosum* subsp. *pautense* seem to have lost the lowland species' mericarp elaborations which are probably of advantage for animal-dispersal and have become adapted to higher elevations. As a result there has been some convergence in characters in the two taxa, reflected in the numerical analysis.

Closest to section *Tomentosum* is section *Amblyphyllum* (Fig. 18E), composed of the two species *Malvastrum amblyphyllum* and *M. grandiflorum*. While sharing many characters with the last section, these two species differ particularly in their less specialized inflorescences and more specialized mericarps. The mericarps are narrowly winged on their distal margins and the flowers are among the few whose styles do not recurve when the petals wilt. The two species in this section share 44 (or 73%) of the 60 characters examined.

The section *Malvastrum* is composed of four taxa in two species (Fig. 18F). The numerical analysis has shown that *M. aurantiacum* and *M. coromandelianum* are related, though distantly. These are the only two species in which the apical cusp is remote from the proximal margin. The section probably had its origin in the lowland Paraná basin of South America. The most closely allied section to the section *Malvastrum* according to the numerical analysis is the section *Amblyphyllum*.

The seventh section is the section *Corchorifolium* composed of the single species *Malvastrum corchorifolium* (Fig. 18G). Morphological and chromosomal evidence summarized in Table 4 as well as observations of living plants from various areas of its range have convinced me that this species has resulted from allopolyploidy in a hybrid between *M. americanum* and *M. coromandelianum*. This connection has been indicated in Fig. 18 by a dotted line. The octoploid chromosome number ($2n = 48$) as well as its range, combined with the large number of intermediate characters present in *M. corchorifolium*, support this hypothesis. The species probably arose after chance hybridization occurred between the two pre-

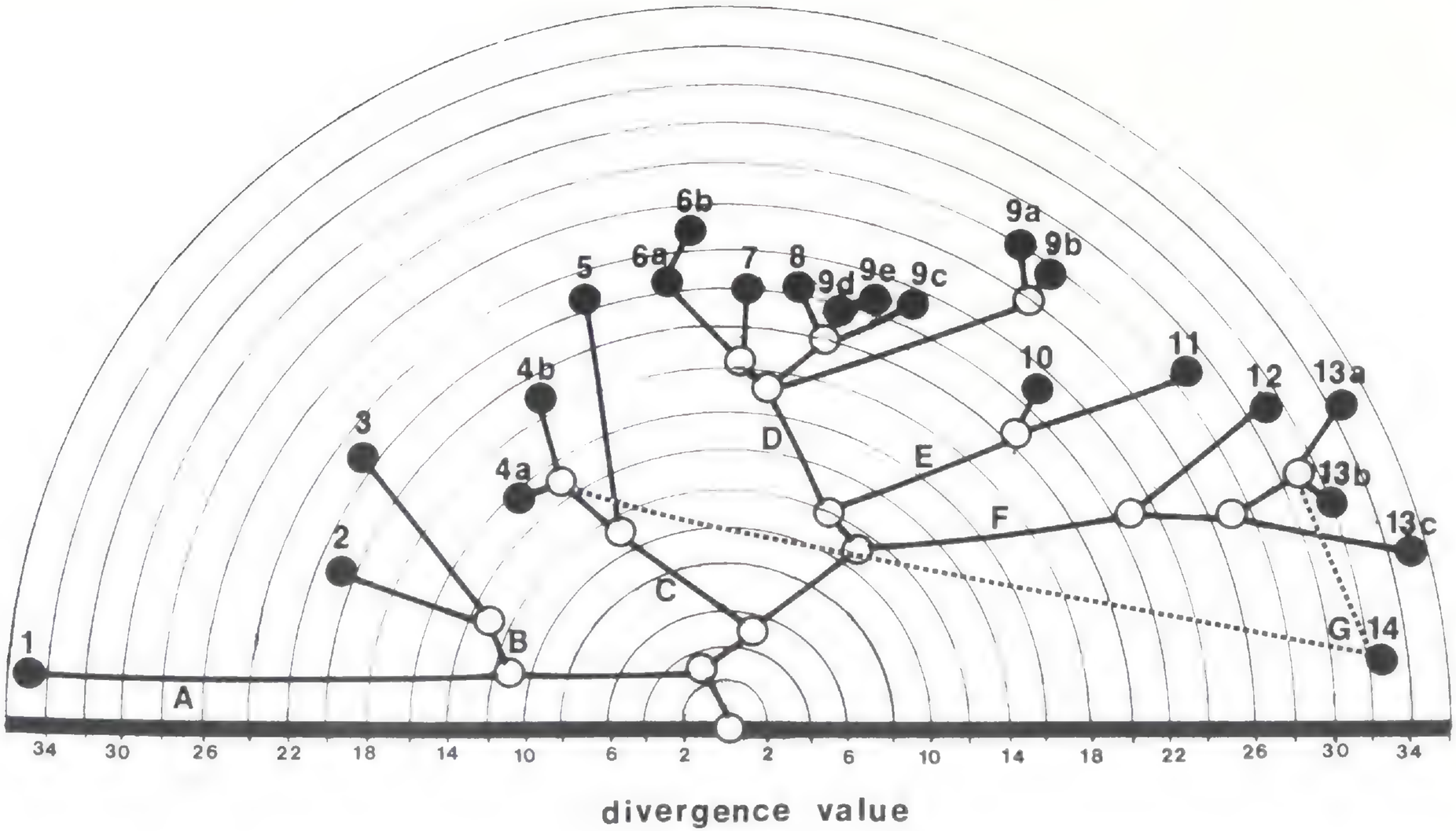


Figure 18. Wagner Tree for *Malvastrum*. A. Section *Sidopsis*. B. Section *Interruptum*. C. Section *Americanum*. D. Section *Tomentosum*. E. Section *Amblyphyllum*. F. Section *Malvastrum*. G. Section *Corchorifolium*. Open circles indicate hypothetical ancestors plotted at points of shared primitive characters. See appendix II for OTU code explanation.

Table 4. **Evidence for allopolyploid origin of *M. corchorifolium***

Character	*M. americanum* var. *americanum*	*M. corchorifolium*	*M. coromandelianum* subsp. *coromandelianum*
chromosome number	$2n = 24$	$2n = 48$	$2n = 24$
filament column length	2.03 mm	2.02 mm	1.95 mm
column vesture	pubescent	1–3 hairs	glabrous
pollen size	49–60 μm	66–89 μm	70–91 μm
carpel number (mean)	13	12	11.5
mericarp height	1.8 mm	1.9 mm	3.0 mm
mericarp length	2.4 mm	2.8 mm	3.0 mm
endoglossum	present	present, but small	absent
calyx-lobe length	5.9 mm	5.5 mm	4.9 mm
calyx vesture (adaxial)	simple and 5 8-radiate, 2 sizes	simple and 4–8-radiate, 2 sizes	simple (margins only), 2 4-radiate, 1 size or gradational
bracteole length (mean)	6.6 mm	5.6 mm	5.1 mm
pedicel length at anthesis (mean)	0.1 mm	1.0 mm	1.9 mm
bifid floral bract	always present	often present	absent
first flowering	16–20 weeks	12 weeks	6 weeks
daily anthesis (local comparison)	5–6:30 pm	4–6 pm	4–5:30 pm
inflorescence type	dense terminal spike, lowest 1–3 flowers remote, sessile	terminal spike, lowest 4–6 flowers solitary-axillary, subsessile	solitary-axillary, pedicellate
leaf vesture (adaxial)	5–6-radiate	4–5-radiate	simple
branching	single main stem, branching in upper 1/3 to 1/2	single main stem, branching in upper 1/2	several main stems (in age), branching near base

sumed parents in Central America where they had become sympatric after the emergence of the land bridge. Both *M. americanum* and *M. coromandelianum* have a gametic chromosome number $n = 12$, and while the hybrid is probably not fertile there are no barriers to gametic exchange. The three species occur together in the region of Nicaragua, Honduras, Guatemala, and Chiapas, Mexico, as well as in certain parts of the Caribbean. Being an autogamous species, *M. corchorifolium* has apparently persisted and even expanded its range as a result of a greater tolerance to semi-arid conditions and to areas of brackish and limestone soils than is shown by the other two species.

While hybridizations were attempted among the species raised in the greenhouse, the results were inconclusive for the most part. Often, flowering of a given taxon was not coincident with anthesis in other taxa. Nevertheless, the more significant difficulty was that of technique. Since anther dehiscence occurred before or as the flowers opened, emasculation in bud was necessary to prevent self-pollination. However, this was difficult to accomplish without damage to the flower, not only because of their often small size in bud, but also because the exposed flower-parts were too delicate to withstand drying after the calyx-lobes and petals had been removed. Crossing was most effectively accomplished in species whose flowers bore stigmas that were exserted from the anther-cluster. Sixty-two crosses were performed in 1978, and the resultant seeds were planted early in 1979. As indicated in Table 5, wherein the female parent is listed first, fruit set varied from 0–10% success to 80–100% success. Although the results are based on fruit set alone, a few tentative conclusions may be drawn. *Malvastrum corchorifolium, M. interruptum,* and *M. grandiflorum* seem to be the most isolated species – the former two as a result of high ploidy levels and the latter probably as a result of unknown incompatibility factors. I would speculate that the elongated style in *M. grandiflorum* may make the ovary inaccessible to pollen grains of other taxa with short pollen-tubes. Of the 886 seeds produced from successful crosses and planted, only 21 seeds (2%) germinated. Of these 21 individuals, six died soon after germination. The 15 survivors resulted only from the crosses showing 80–100% success listed in table 5. The successful crosses help support the phylogeny proposed (e.g., the apparent success of the *M. amblyphyllum* × *M. grandiflorum* cross presents

Table 5. **Hybridization results based upon % fruit set**

Parentage	Seed sources
0–10% Success	
M. americanum × *M. corchorifolium*	*Hill 7640 × Lakela 27892; Silva-Santos 28017 × Steere 1010*
M. coromandelianum × *M. corchorifolium*	*Morel 8095 × Correll 43834; Hill 4579 × Seymour 5442*
M. interruptum × *M. amblyphyllum*	*Gutiérrez 357 × Krapovickas 18558*
M. interruptum × *M. coromandelianum*	*Gutiérrez 357 × Corral-Lorenzoni 13; Gutiérrez 357 × Board 1106a*
M. interruptum × *M. corchorifolium*	*Gutiérrez 357 × Proctor 18585*
M. interruptum × *M. grandiflorum*	*Gutiérrez 357 × Krapovickas 19300*
M. grandiflorum × *M. americanum*	*Krapovickas 19300 × Hill 7640*
M. grandiflorum × *M. bicuspidatum*	*Krapovickas 19300 × Bye 6940*
M. grandiflorum × *M. coromandelianum*	*Krapovickas 19300 × Hill 4579*
30 – 50% Success	
M. americanum × *M. coromandelianum*	*Hill 6054 × Fryxell 720a; Hill 6054 × Corral-Lorenzoni 13*
M. americanum × *M. grandiflorum*	*Hill 7640 × Krapovickas 19300*
M. bicuspidatum × *M. coromandelianum*	*Bye 6940 × Corral-Lorenzoni 13; Lehto 19487 × Hill 4579*
M. coromandelianum × *M. grandiflorum*	*Percival s.n. × Krapovickas 19300; Breedlove 20019 × Krapovickas 19300*
80–100% Success	
M. amblyphyllum × *M. grandiflorum*	*Krapovickas 18558 × Krapovickas 19300*
M. aurantiacum × *M. coromandelianum*	*Hill 6430 × Corral-Lorenzoni 13; Hill 6430 × Hill 4579*
M. coromandelianum subsp. *coromandelianum* × *M. c.* subsp. *capitatospicatum*	*Board 1106 × Varela 52*
M. bicuspidatum subsp. *bicuspidatum* × *M. b.* subsp. *campanulatum*	*Bye 6940 × Waterfall 13918*

further evidence supporting the close relationship of the two species). While infertility may explain the low percentage of seed germination, seed dormancy is another likely explanation.

My conclusion resulting from these hybridization attempts is that, while the subspecies are capable of interbreeding, the species of *Malvastrum* are effectively isolated from one another, a conclusion also supported by the lack of intermediate specimens in herbaria.

To summarize, speciation in *Malvastrum* has resulted from two processes in particular: 1) autopolyploidy or allopolyploidy, and 2) geographic isolation. Geographic isolation has resulted from 1) geologic and climatic changes and from 2) discontinuous dispersal of the fruits by means of animal transport. Several lineages or sections are now indicated by the data accumulated during the course of this study of *Malvastrum*.

Intergeneric relationships

During the early period of *Malvastrum* classification a very few morphological characters were used to show its alliance with other genera in the Malvaceae. Gray in Sprague & Gray (1849, p. 47) assigned *Malvastrum* to the tribe Malveae and placed the genus in the subtribe Sideae Presl. The stigmas of all of the members of this subtribe were said to be capitate. Alefeld (1862) proposed the tribe Malvastridae, typified by *Malvastrum*, and placed the tribe within the subfamily Sideae. Members of the new tribe had mericarps bearing solitary ascending ovules, and the subfamily Sideae was separated from the subfamily Malveae by its capitate rather than decurrent stigmas. The tribe Malvastridae included four genera: *Palaua* Cav., *Malvastrum* A. Gray, *Kitaibelia* Willd., and *Diplopenta* Alef. (= *Pavonia* Cav.). *Malvastrum* was assigned to the tribe Malveae by Bentham in Bentham & Hooker (1862), where it has remained. The genus was further placed in the subtribe Eumalveae (= *Malvinae*) together with *Althaea* L., *Lavatera* L., *Malva* L., *Callirhoe* Nutt., *Sidalcea* A. Gray, and *Napaea* L. and was distinguished from these by its capitate and not decurrent stigmas. The solitary ascending ovule and single series of carpels defined the subtribe. Schumann (1890) also concluded that the ascending ovule was a very important taxonomic character in the tribe Malveae and also placed *Malvastrum* in the subtribe Malvinae, also noting its exceptional capitate rather than decurrent stigmas. Kearney (1951b) also considered the importance of the capitate stigmas and ascending ovules in *Malvastrum* but, for the first time, realized that it and other uniovulate genera were closely allied to certain pluriovulate genera. As a result, *Malvastrum* and 17 other genera were assigned to the subtribe Abutilinae.

Classification within the tribe Malveae is currently in a state of flux. Bates (1968, 1969) and Bates & Blanchard (1970) have

proposed 16 "alliances" of genera that are thought to represent at least three major evolutionary lines. Until more information is accumulated, formal taxonomic status cannot be given to the alliances. Chromosome numbers have been used as a basis for the re-evaluation of previous classification systems. Bates & Blanchard (1970) have pointed out that the major evolutionary trends in morphology within the tribe have been reductional. This includes sequences such as those leading from a woody to a herbaceous habit and a general reduction in the size and complexity of floral organs. In contrast, specializations have occurred in a few organs, such as in the mericarps, leading to more effective seed dispersal. One of the greatest problems in determining phylogeny within the Malveae is the occurrence of similar reduction series in separate lineages. In particular, the similarity in mericarps in several unrelated genera have led to the taxonomic confusion in *Malvastrum*.

Bates & Blanchard (1970, p. 929) have proposed that a very significant event in the evolution of the Malveae was the early establishment of base chromosome numbers of $x = 7$, 6, and 5 through aneuploid reduction from a probable base-number of $x = 8$. Again, a single line is not indicated and so species with a like base-number are not necessarily related. Elaboration of the base-number has occurred in several genera through euploidy and aneuploidy and still other changes are thought to have occurred by means of hybridization between species with different base-numbers.

Malvastrum is considered to be in a line separate from the other alliances, and has no close relatives. The basic chromosome-number $x = 6$ is shared only by members of the *Gaya* alliance (*Cristaria* Cav., *Gaya* Cav., and *Lecanophora* Spegazzini) and by *Malacothamnus chilensis* (Gay) Krap. whose generic placement is uncertain. The occurrence of $x = 6$ in the three otherwise divergent groups is most likely coincidental and does not indicate a common ancestry. Therefore, intergeneric relationships concerning *Malvastrum* cannot be based upon chromosomal evidence as yet.

Malvastrum, like the other uniovulate Malveae, probably has been derived from early pluriovulate members of the tribe with pseudocapsular loculicidally and septicidally dehiscent fruits. In this regard the mericarps of several species of *Malvastrum* retain a complete or incomplete loculicidal dehiscence, most frequently along the proximal-apical margin. The ancestral group also seems to have had two-chambered fruits partitioned by an endoglossum.

In time, all of the ovules with the exception of the single ascending basal ovule in the lower chamber were lost and the upper chamber with its associated endoglossum was likewise reduced or lost. A highly reduced upper chamber bounded beneath by a minute endoglossum remains in several species of *Malvastrum*. The ancestral entity from which *Malvastrum* was derived likely had yellow flowers and the calyx undoubtedly was subtended by a spirally arranged tribracteolate involucel, characters shared by all of the contemporary species. The base chromosome number $x = 6$ was probably derived by reduction from a higher number of $x = 7$ or 8 and, once established, was subsequently modified by euploidy in the genus.

No other contemporary genus has such a combination of characters. A similar but less extreme reduction series in the mericarp has occurred in *Sphaeralcea* but the different basic chromosome-number ($x = 5$), the frequent occurrence of more than one ovule in the mericarp, and the frequently mauve or salmon-orange corolla color as well as other characters suggest that the two genera have been separate for a long period. Nevertheless, when all of the Malveae are examined, there is a degree of morphological coherence between the *Sphaeralcea* and *Malvastrum* alliances, both of which seem to have originated in South America. The ancestry of the two alliances should probably be sought in the diverse, comparatively primitive *Abutilon* alliance whose members, while individually often specialized, frequently retain pluriovulate loculicidally and septicidally dehiscent schizocarpic or pseudocapsular fruits. Within the alliance, genera such as *Wissadula* Medicus, *Briquetia* Hochreutiner, *Dirhamphis* Krapovickas, *Batesimalva* Fryxell, *Bastardiastrum* Bates, and *Allowissadula* Bates possess a well-developed two-chambered mericarp, but the basal ovule is pendulous. Within *Anisodontea* Presl, paired with *Lavatera* in its own alliance (Bates & Blanchard, 1970), both two-chambered pluriovulate and single-chambered uniovulate mericarps are found, demonstrating that the different reductional states can occur in a single genus. It is interesting to note that in the pluriovulate species of *Anisodontea* the basal ovule is pendulous, while in the uniovulate species the ovule is ascending. I cannot now assess the probability that the ascending ovule in *Malvastrum* is a primitive condition or that the ovule changed its orientation as the mericarp was reduced.

To be continued in Vol. 84, Nos. 838 & 839 (April & July, 1982).

EXPERIMENTAL TAXONOMY IN THE GENUS *AMELANCHIER*. II: DO THE TAXA IN THE GENUS *AMELANCHIER* FORM AN AGAMIC COMPLEX?

W. Ann Robinson

According to Wiegand (1912) our major herbaria contained almost as many transitional sheets as sheets typical of the supposed species in the genus *Amelanchier*. In fact, many taxonomists have been inclined to believe that no specific lines exist in this genus. McVaugh (1946) stated:

> "the multiplicity of forms in *Amelanchier* (as also in *Crataegus, Malus, Rubus* and other genera) is so great as to defy taxonomy based on herbarium material alone. I think we shall not arrive at any satisfactory scheme of classification of these genera until we know more about their genetical peculiarities."

With this goal in mind the following hypothesis is suggested. The taxa in the genus *Amelanchier* form an agamic complex not unlike that existing within several genera of the Maloideae: *Crataegus, Malus,* and *Sorbus*. Babcock and Stebbins (1938) suggested that the only basis for a satisfactory treatment of agamic complexes was an understanding of the role that the three processes, polyploidy, hybridization, and apomixis have played in their formation.

Polyploidy is considered to have played a prominent role in the evolution of this genus as diploid, triploid, and tetraploid forms commonly appear in the *Amelanchier* of the northeastern United States (Robinson & Partanen, 1980).

Experimental studies into the breeding methods of *Amelanchier,* however, have been relatively meager. Both Wiegand (1912) and Nielsen (1939) described from field observations the apparent ease with which the species of *Amelanchier* hybridize; neither, however, performed confirmatory experiments. Cruise (1964) measured the extent of hybridization in three eastern *Amelanchier* species with the utilization of Anderson's hybrid index. Harris (1970) reported that interspecific crosses have been performed at the Beaverlodge Experimental Station with *Amelanchier alnifolia* Nutt., the common species of the western United States, but the experimental data

were not included in this paper. Harris (1970) also suggested that most plants of *A. alnifolia* are self-fertile.

Kirshner (1890) may have been the first to suggest self-fertility in *Amelanchier* when he wrote: "In den schräg stehenden Blüten kann spontane Selbstbestaubung leicht durch herabfallenden Pollen erfolgen." McKay (1973) indicated that self-compatibility existed in several of the eastern *Amelanchier* species from observations of plants naturally occurring in Ontario, Canada. Her experiments, however, are not completely comparable to the present study, for emasculation involved only removal of the anthers, and the types of self-compatibility, autogamy and geitonogamy, were not differentiated.

The question of apomixis in *Amelanchier* has had few published references. McVaugh (1946) suggested parthenogenesis as a possible explanation for the confusion in this genus. McKay (1973) emasculated 43 flowering *Amelanchier* racemes and found 12 percent of the racemes showed successful seed set. Her experiments, however, did not differentiate parthenocarpy with aborted seeds from apomictic seed formation. In 1974 Robertson made the statement that, unlike *Crataegus,* apomictic clones are not known in *Amelanchier.* Since *Sorbus* and *Malus* were reported by Stebbins (1941) to have SA + P (somatic apospory + parthenogenesis) type of apomixis, the experiments in this paper were formulated to test for its existence in the genus *Amelanchier.*

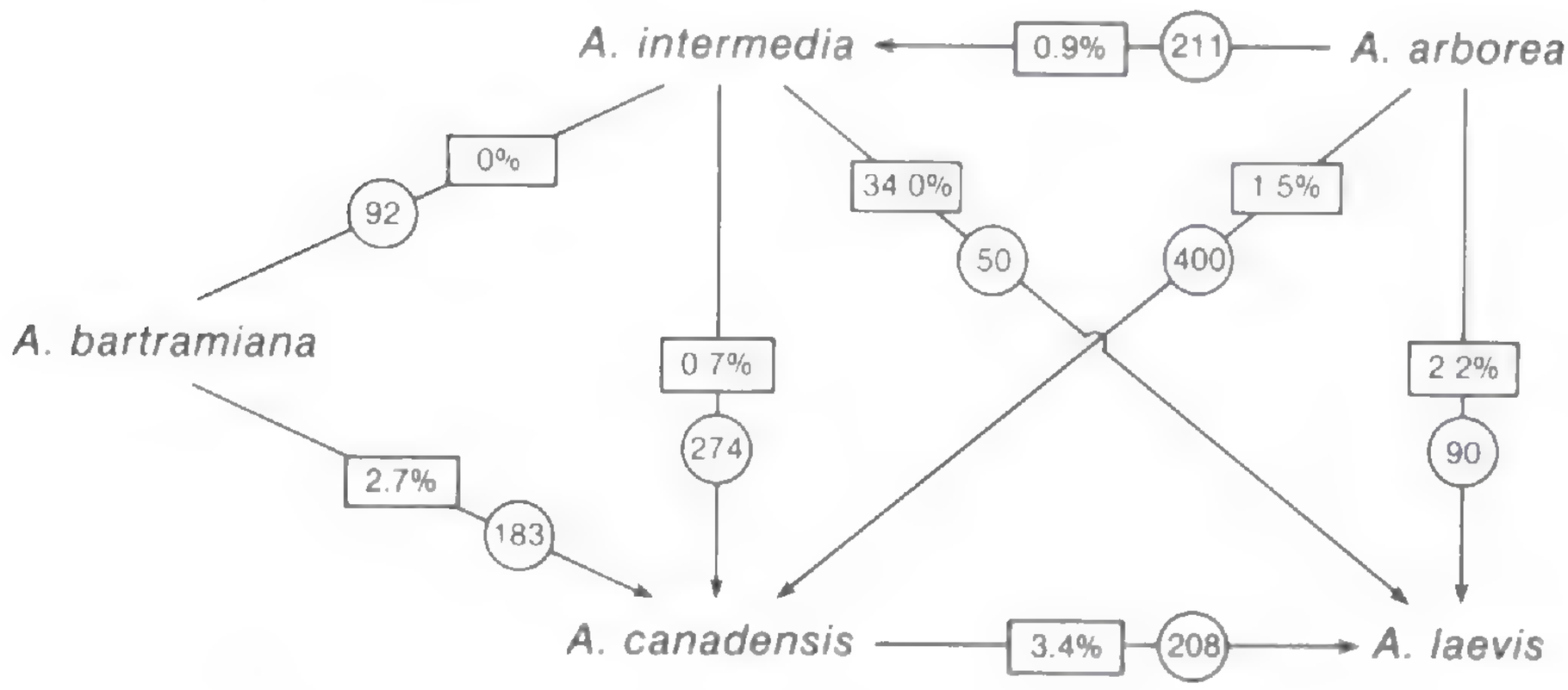
PROCEDURE

Considering that the number of species comprising *Amelanchier* is unsettled, it seems wisest to follow the taxonomy of Fernald (1950), who recognized the most species in the northeastern United States. This should afford the greatest amount of expected genetic variation. The validity of these species will be explored in future studies. The experiments in this study have therefore been confined to the following species:

A. amabilis Wieg.
A. arborea (Michx.f.) Fern.
A. bartramiana (Tausch) Roemer
A. canadensis (L.) Medic.
A. gaspensis (Wieg.) Fern. and Weath.
A. humilis Wieg.

A. intermedia Spach
A. laevis Wieg.
A. nantucketensis Bickn.
A. obovalis (Michx.) Ashe
A. sanguinea (Pursh) DC.
A. stolonifera Wieg.
A. wiegandii Nielsen

Figure 1
Hybridization trials with the species of the Canadensis complex



——— A line between two species indicates that cross-pollination has resulted in fruit set. (If not reciprocal, arrow points to pistillate parent).

Absence of a line between two species indicates that cross-pollination has resulted in no fruit set.

[ ] The number in the rectangular box denotes the percentage of flowers resulting in successful fruit set, with normal seed formation.

[?%] A question mark preceding the percent indicates fruit was set, but it was damaged by predators.

( ) The number enclosed in the circle indicates the number of flowers that were cross-pollinated.

The original goal was to collect one living plant of each species and more if possible. These were moved, beginning in 1970, to Monroeville, Pa. where ecophenic variation would be minimized in a uniform environment. By separation of a portion of the stoloniferous clump or by division of the fastigate forms one can readily transplant specimens of *Amelanchier*, with the new and former specimens continuing good growth. The original collection sites of the plants utilized in this study are enumerated in the appendix. Voucher specimens of all material utilized have been deposited in the Carnegie Museum Herbarium (CM).

There has been a 67.9% survival rate following transplantation, with a total of 40 plants presently under observation. Unfortunately, two plants of *Amelanchier gaspensis* died before experiments could be performed and this species could not be included in the present study. A single plant of *A. amabilis* was successfully transplanted but has yet to flower. Transplantation frequently appears to delay flowering by three to four years.

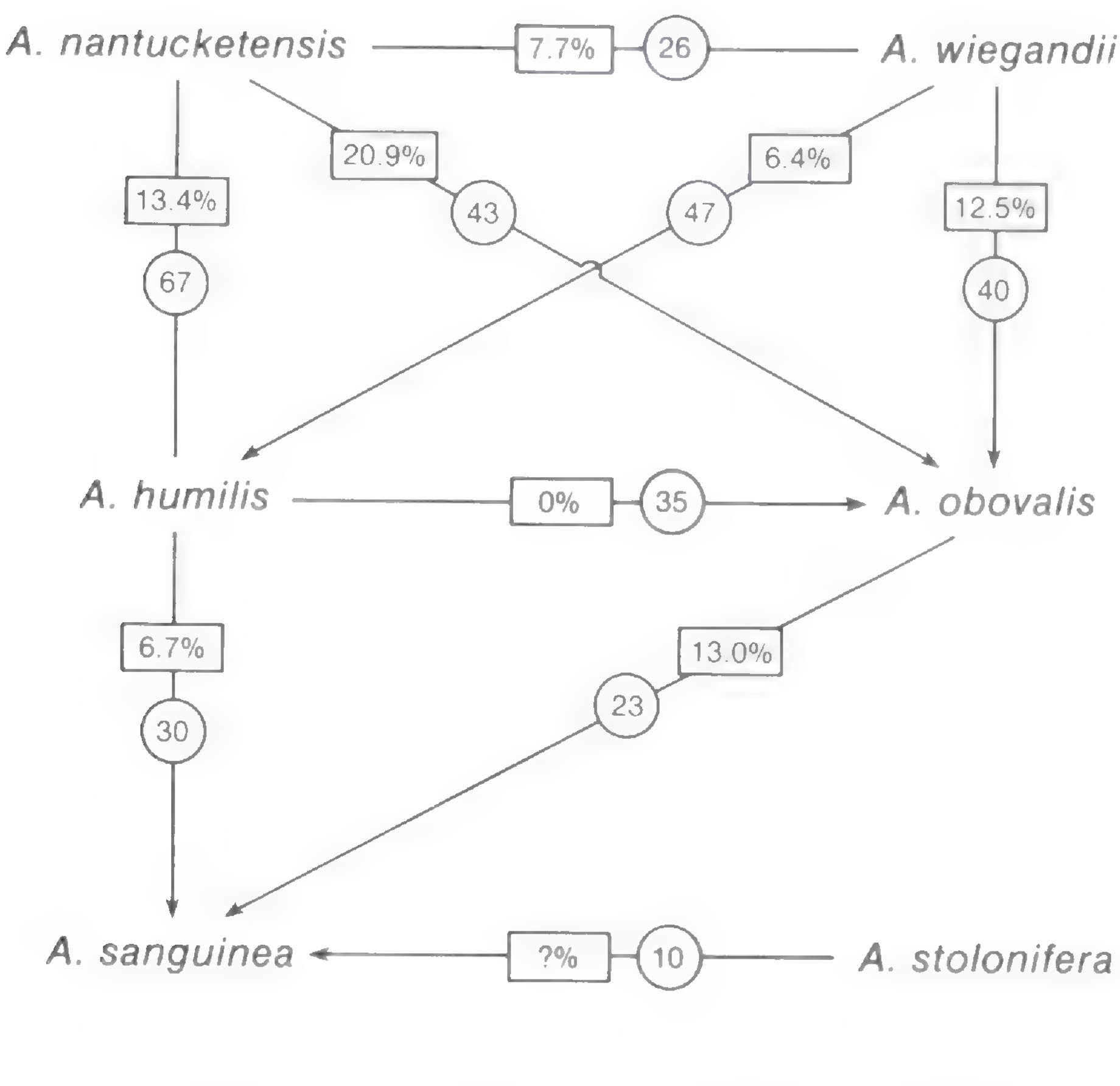
If hybridization is as common as suspected in *Amelanchier*, there exists the possibility that plants of hybrid origin, or plants having undergone introgression, could have been introduced into cultivation. Close morphological observations and pollen stainability with cotton blue in lactophenol were utilized as indicators of possible hybridization. All specimens suspected as being of hybrid origin were eliminated from the breeding experiments, except for plants of *A. wiegandii* and *A. sanguinea*, with 39.3% and 37.6% pollen stainability respectively. These plants were retained in the study with the thought of evaluating their relationships to the other species and with the prospect of a review of their evolution and taxonomic status.

As the routine morphological observations were made, the plants appeared to fall into two morphological complexes (Robinson & Partanen, 1980). *Amelanchier bartramiana*, with its distinctive single or few flowered raceme, does not fit comfortably in either complex but is included in the Canadensis complex because of its diploid nature.[1] The morphological traits appear to be correlated with a change in ploidy level, the Canadensis complex representing diploid taxa and the Sanguinea complex triploid and tetraploid taxa. The only taxa observed to be exceptions to this hypothesis are *A. intermedia* and *A. obovalis* in which both diploid and triploid plants are found.

The following procedure was utilized in all the experiments to investigate the possible existence of apomixis, self-compatibility, and hybridization in the *Amelanchier* taxa growing in the northeastern United States. When autogamy was investigated, it was without emasculation and without the application of pollen. Single flowers were covered by bags constructed of seamless cellulose dialysis tubing, at least 48 hours prior to anthesis. The dialysis bag, in this case and in all the experiments to be enumerated, remained in

[1]Löve and Löve (1966) have reported tetraploid individuals.

Figure 2
Hybridization trials with the species of the Sanguinea complex[3]



[3]*A. stolonifera* × *A. obovalis* and *A. stolonifera* ×*A. wiegandii* have not been attempted.

place until pollination was complete. This is extremely important for although *Amelanchier* has been considered entomophilous and allophilic (Cruise, 1964), experiments by Landridge (1969) have indicated significant airborne pollen in the closely related genus *Malus*. Upon removal of the dialysis bag, a bag constructed of fiberglass screening was substituted. This is necessary for the collection of dehisced immature fruit and for protection against predators seeking partially ripe fruit. *Amelanchier* has been noted to experience the "June Drop" phenomenon found in other Maloideae (Heinicke, 1917).

To test for apomixis, geitonogamy, xenogamy, and interspecific hybridization, emasculation was performed 48 hours prior to anthesis. Although the northeastern United States taxa of *Amelanchier* are largely protogynous[2], occasionally the anthers dehisce prior to anthesis. Kenneth Robertson and Robert Simonet (both pers. comm.) also metioned this possibility. When any evidence of early anther dehiscence was noted at the time of emasculation, the flowers were not utilized in the experiments. Emasculation involved removal of the superior floral cup (sepals, petals, and stamens) under magnification with a cutting edged needle. Such emasculation is much more feasible, rapid, and reliable than simply removing the anthers. Nyéki (1974) found no significant difference between fruit set in pear flowers subjected to radical emasculation, and those deprived only of their anthers. Immediately following emasculation the pollen appropriate to the experiment was applied utilizing the entire stamen removed from the isolation of a dialysis bag. The filament was held by tweezers and the dehisced anther brushed against the stigmas. The racemes were then enclosed in a dialysis bag. The pollen applied following emasculation remains on the stigma and is ready to germinate as soon as conditions are favorable. It was impossible because of the varying number of flowers available on the plants and the varying flowering times to have identical numbers of flowers of each plant species for the individual experiments. The data are summarizations of experiments performed different years, various days, and numerous times of the day.

Seed germination was tested initially in the laboratory. Fungal growth proved to be a marked problem even after cleaning by agitation, surface disinfectants, and fungicides. Since the factors involved in breaking dormancy can be quite complex and since germination in these early experiments never exceeded 8.1%, the decision was made to follow the normal stratification pattern presently successfully undergone by seeds under the influence of the vagaries of the weather in the north temperate zone.

All seeds were planted in sifted soil in peat pots and placed directly in the ground soon after they would have normally fallen to the ground. Seedlings do not appear until the following spring.

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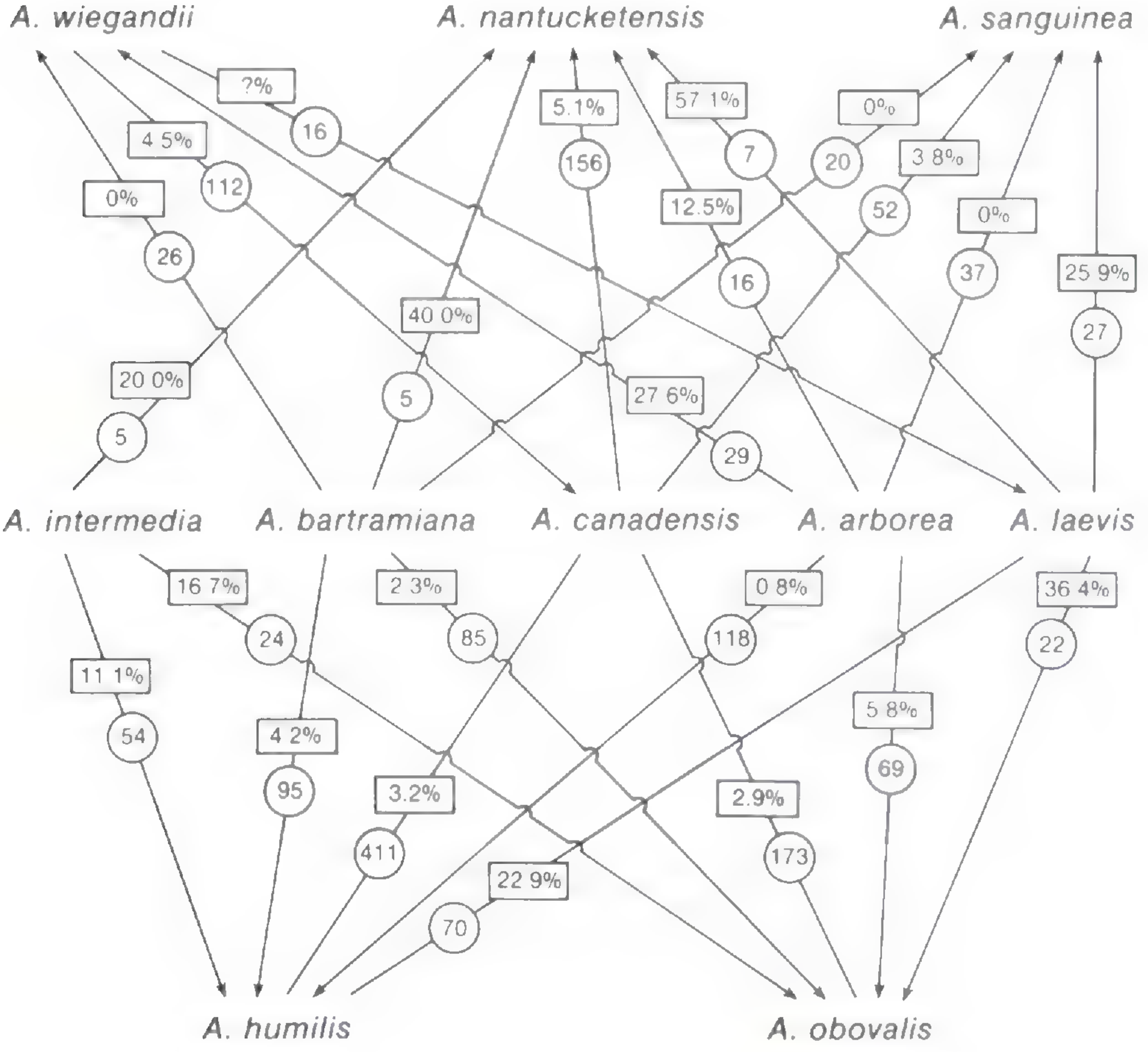
[2]In Europe *A. canadensis* (*A. botryapium* DC.) was noted to be slightly protogynous by Kirshner (1890).

Figure 3
Hybridization trials between the species of the Sanguinea complex and the species of the Canadensis complex



A list of parental samples and results of individual crosses is available on request from the author.

RESULTS

Prior to 1977, only one species, *A. humilis,* formed fruit with apparently mature seed following emascuation to test for apomixis. Of the 1731 flowers of *A. humilis* emasculated only 0.58% formed fruit with mature seed, and this seed failed to germinate. Since this exceedingly low figure could have been in the range of experimental error, during the 1978 and 1979 seasons, these experiments were markedly extended. In 1979 one added technique was initiated. Following emasculation and prior to covering with the dialysis bag, the stigmas were dusted with the pollen of *Tussilago farfara* L. This

species-alien pollen was selected due to its abundant availability at the time of flowering. This technique was adopted since Frankel and Galun (1977) had reported that the stimulation of pollination is required for apomictic seed development in apple. In 1978 and 1979 a total of 2100 flowers were emasculated with no resulting fruit formation with mature seed. It therefore seems reasonable to assume that the SA + P type of apomixis does not occur in the northeastern forms of *Amelanchier*.

The results of the experiments to check for the two types of self-compatibility are shown in Table 1. First, it is important to state that all the plants in this study have had fruit production with normal seed following open-pollination. Therefore, we are investigating plants with a potential for seed formation under the appropriate conditions. Plants of *Amelanchier arborea* and *A. stolonifera* produced no fruit with normal seed following autogamous and geitonogamous pollination. The attempted pollinations of *A. stolonifera* are too few to make any positive statement. However, in the case of *A. arborea* it can be stated with a degree of subjectivity that the specimens investigated in this study are self-incompatible. Although it is difficult to discern with absolute accuracy (see Table 1), it appears that the Sanguinea complex has a higher potential for self-compatibility than the Canadensis complex. This is even more apparent from the seed germination attempts (Table 2). The seeds resulting from autogamous and geitonogamous pollinations within the Canadensis complex failed to germinate. Within the Sanguinea complex, seedlings of *A. obovalis* and *A. humilis* from autogamous pollinations and *A. nantucketensis* from a geitonogamous pollination are presently growing. A seedling of *A. wiegandii* from a geitonogamous pollination died the summer following its germination.

Comparing the results of the xenogamous pollinations with those of autogamy and geitonogamy, the overall impression emerges that xenogamous pollinations result in a higher percentage of normal seed. It should be noted (Table 1) that *A. arborea* still did not form normal seed, but following xenogamous pollination fruit did form but with immature and aborted seeds. The seedlings from the xenogamous crosses are double the number from self-compatibility crosses and crosses between species and are generally healthy and vigorous. There are five seedlings from *A. humilis* × *A. humilis* and six seedlings from *A. canadensis* × *A. canadensis* crosses.

Table 1
Optional breeding methods

Species	Types of pollination					
	Autogamous		Geitonogamous		Xenogamous	
	No. flowers pollinated	No. resulting fruit with mature seed	No. flowers pollinated	No. resulting fruit with mature seed	No. flowers pollinated	No. resulting fruit with mature seed
Canadensis complex						
A. arborea	84	*	81	*	98	0**
A. canadensis	234	3	296	3	364	35
A. intermedia	54	4	57	9	36	2
A. laevis	36	1	98	10	15	***
A. bartramiana	12	2	22	3		
Sanguinea complex						
A. humilis	111	26	46	6	173	22
A. nantucketensis	15	0**	12	4	12	5
A. obovalis	46	6	14	5	73	13
A. sanguinea	4	1	44	***		
A. stolonifera	1	*	6	*		
A. wiegandii	5	1	16	6		

* All flowers dried up
** Fruit with immature and aborted seeds
*** Fruit set, but destroyed by predation

Table 2. **Results of germination trials with seeds from autogamous, geitonogamous, and xenogamous pollinations**

	autogamous		geitonogamous		xenogamous	
	Total No. Seeds	No. Seeds Germinated	Total No. Seeds	No. Seeds Germinated	Total No. Seeds	No. Seeds Germinated
Canadensis complex						
A. canadensis	3	0	12	0	84	7
A. intermedia	5	0				
A. laevis	2	0				
Sanguinea complex						
A. obovalis	9	1	10	0	21	4
A. humilis	40	2	12	0	36	5
A. nantucketensis			23	5	4	0
A. wiegandii	2	0	5	1		
A. sanguinea	1	0				

The results of the interspecific crosses are detailed in figures 1–3. Every combination has been attempted except for two: *Amelanchier stolonifera* × *A. obovalis* and *A. stolonifera* × *A. wiegandii.* The lack of a line between the two species, therefore, indicates fruit did not set following hybridization with the above two exceptions. Considered as a whole, a total of 336 apparently mature normal seed resulted from 3622 interspecific crosses. With the exception of the seeds from the interspecific crosses listed in Table 3, seed germination has failed. One can also note from Table 3 that 54.5% of the seedlings died during the first year. The three hybrid seedlings, *A. canadensis* × *A. arborea,* that grew from seeds planted during the late summer of 1972 have exhibited remarkably rapid growth and vigor. They flowered for the first time in 1977 but have yet to set fruit following open pollination or in experiments to test for apomixis or autogamy. The pollen stainability of the three plants has been 91.9%, 92.6%, and 94.8% respectively, with observations made the same day and hour for each plant.

DISCUSSION

With the possibility that *Amelanchier* taxa form an agamic complex, the three processes considered to operate in such a complex (Stebbins, 1950) will be discussed in turn: apomixis, hybridization, and polyploidy.

On the basis of the experiments in the present study, it can be stated with a reasonable degree of assurance that the SA + P type of apomixis does not occur in the northeastern forms of *Amelanchier.*

Table 3. **Germinated seeds from interspecific hybridization**

Interspecific cross	Total No. Seeds	No. Seeds Germinated	Seedling Survival To 1 Yr.
A. canadensis × *A. intermedia*	4	1	0
A. canadensis × *A. arborea*	22	3	3
A. obovalis × *A. nantucketensis*	13	3	0
A. obovalis × *A. canadensis*	3	1	1
A. obovalis × *A. intermedia*	6	1	0
A. humilis × *A. laevis*	16	1	0
A. wiegandii × *A. arborea*	16	1	1

Muniyamma and Phipps (1979) state that apparently sexual endosperm is necessary in *Crataegus* for apomictic seed development and that *Crataegus pruinosa* (Wendl.) K. Koch, *sens. lat.* has Sa + Ps (somatic apospory + pseudogamy) type of apomixis. Further experiments are being initiated to evaluate its occurrence in *Amelanchier*.

Is it necessary, however, to consider that agamospermy must exist for the presence of an agamic complex in a genus? Following the classification of Gustafsson (1946), vegetative reproduction could be considered an apomictic phenomenon. Perpetuation of unbalanced chromosome forms by self-compatibility and vegetative reproduction, and the similar longevity of hybrid microspecies with occasional fertile gametes and vegetative reproduction, could give the typical morphological appearance of an agamic complex. The discontinuities of the diploid species would be obscured by the hybrid derivatives and polyploids. With the exception of *Amelanchier sanguinea* and *A. wiegandii* the members of the Sanguinea complex have been observed to form stoloniferous clumps. The remaining taxa included in this study can reproduce by shoots from their root systems. Frequently a single dead tree trunk will be replaced by a multi-trunked shrub. Excluding the possiblity of major environmental change all of the taxa in the northeastern United States could maintain themselves by asexual vegetative reproduction.

Following study of the *Amelanchier* specimens from the major eastern herbaria the Wiegand estimation (1912) that a third of the sheets were hybrids soon seems most valid. From field observation, however, a 33% rate of hybridization seems inordinately high. With a search for the unusual and different specimens in *Amelanchier*, plant taxonomists have collected a disproportionate number of hybrids. Hybrids occur with the greatest frequency in the pioneer shrub community in the succession following burning, deforestation, or the abandonment of farm land. Although these areas are more frequent following the activities of man, they are less common than the preferred environment in the forest community of the Mixed Mesophytic Forest Region and the Hemlock-White Pines-Northern Hardwoods (Braun, 1950). Occasionally *Amelanchier* will grow in the relatively shaded understory of the mature forest, but it seems to prefer sun light and less competitive edge communities, such as the abundant hillsides and stream banks found throughout

the northeastern United States. In addition, the results of the present study indicate that although interspecific pollination, fertilization, and seed formation have the potential to occur, hybrid establishment may be a far less common occurrence (Fig. 3 & Table 3). Although the percentage of hybridization is realistically less than 33%, it is a viable evolutionary pattern, and numerous hybrid swarms of *Amelanchier* taxa are found in disturbed and intermediate habitats.

A statement by Levin (1971) should be mentioned. He notes that the failure to take cognizance of the competitive status of pollen from different sources could lead to erroneous conclusions about the facility with which species hybridize or exchange genes in nature. He states that domestic pollen advantage ostensibly is the rule rather than the exception. Knight (1917) and Cooper (1938), however, reached the opposite conclusion from work with apple. They found that pollen tubes from autogamous pollinations grew more slowly than those from intra-varietal crosses. Further research is required before this point can be evaluated in the genus *Amelanchier*.

Studying the species of the northeastern United States, Robinson and Partanen (1980) indicated that *Amelanchier* contains diploid, triploid, and tetraploid taxa. Although the authors noted the frequent appearance of multivalents and univalents at metaphase I, the plants studied set fruit in open-pollination and the pollen stained generally in excess of 85% with cotton blue in lactophenol. Since *Amelanchier* along with the other Maloideae is considered to be a secondary polyploid (Stebbins, 1950), it apparently readily tolerates the loss of an occasional chromosome.

In the present study, however, several factors indicate a reduced gametic fertility of the polyploid taxa probably attributable to abnormal chromosome segregation. In figure 3 one notes that the role of the pistillate parent is achieved almost exclusively by the polyploid taxa of the Sanguinea complex in crosses with the diploid taxa. This probably reflects a reduced viability of the microgametes of the polyploid taxa, a phenomenon noted by Darlington (1937). In addition, the apparent higher potential for self-compatibility (Table 1) and vegetative reproduction in the polyploid Sanguinea complex could have resulted from the selective advantage of these types of reproduction to plants with reduced viability of microgametes.

Although caution is necessary when studying only a portion of

the taxa in a genus of world-wide North Temperate distribution, the overall impression is emerging that the species of the genus *Amelanchier* represent an agamic complex with polyploidy, hybridization, and asexual vegetative reproduction being major forces in its evolution. The present studies will be extended beyond a regional basis and it is hoped that a clearer picture of the problem will emerge. In this regard, the author would be pleased to receive semi-dried fruit of all *Amelanchier* taxa from documented sources world-wide for propagation and experimentation.

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APPENDIX

List of and collection data for the taxa utilized in this study. (R) = the author's collection.

A. amabilis Wieg. N.Y., Ontario Co., 2.5 mi. S. of Vine Valley, *R 163*

A. arborea (Michx.f.) Fern. W. Va., Jefferson Co., Key's Gap, *R 93;* Pa., Fayette Co., 4.1 mi. S. of Elliottsville, *R 108*

A. bartramiana (Tausch) Roemer Pa., Monroe Co., shore of Lake Naomi, Naomi Pines, *R 120*; Pa., McKean Co., 5 mi. W. of Kane, *R 168*

A. canadensis (L.) Medic. N.J., Ocean Co., off Rt. 539, 3.6 mi. S. of Rt. 72, *R 111*; N.J., Ocean Co., off Rt. 539, 0.1 mi S. of Rt. 530, *R 113*; N.J., Burlington Co., off Rt. 537, 2.8 mi. W. of Ocean Co. Line, *R. 114*; N.J., Ocean Co., off Rt. 537, 0.3 mi. W. of intersection of Rts. 537 and 526, *R 115a*; N.J., Middlesex Co., within cloverleaf of intersection of Rts. 18 and 9, *R 116*; Maine, York Co., Berwick, *O.M. Neal, Jr. 131*; Mass., Norfolk Co., crest of Blue Hill, Milton, *R 157*; Va., Henrico Co., at intersection of Rt. I64, Highland Springs, *R 159.*

A. gaspensis (Wieg.) Fern. and Weath. Maine, Aroostook Co., off Rt. 210, ¼ mi. E. of Rt. 1, Presque Isle, *Margaret Hurst 145.*

A. humilis Wieg. W. Va., Monongalia Co., Old Kingwood Pike, *Dr. and Mrs. H. A. Davis 132;* Maine, Penobscot Co., N. W. side of Rt. 43, 2 mi. off Rt. I95 at Old Town Exchange, *R 148.*

A. intermedia Spach Pa., Pike Co., off Rt. 6, 5.7 mi. E. of junction of Rt. 6 and Rt. 739, *R 119.*

A. laevis Wieg. Pa., Susquehanna Co., Old McConnell farm, near Lakeside, *R 124;* Pa., Bedford Co., Wolf Swamp, Hyndman Quadrangle, 39°52′30″ and 78°44′30″, *R 160;* W. Va., Randolph Co., Red Run, W. of Cheat Bridge, *R 161b.*

A. nantucketensis (Bickn.) Mass., Nantucket Co., Nantucket Isl., Nantucket R. R. bed, near Inquirer-Mirror office building, *R 155*; Conn., New London Co., N. E. side bridge Alewive Cove, Waterford, *R 156.*

A. obovalis (Michx.) Ashe Pa., Lackawanna Co., cliff overlooking DLWRR, ½ mi. E. of Old Forge, *R 122a*; 500′E. of *R 122a, R 122b*; Pa., Luzerne Co., off Rt. 307, crest Penobscot Knob, *R 123a.*

A. sanguinea (Pursh) DC. W. Va., Pendleton Co., North slope North Fork Mt., *R 128 b.*

A. stolonifera Wieg. Maine, Waldo Co., Fort Point, Cape Jellison, Stockton Springs, *R 149.*

A. wiegandii Nielsen Maine, Waldo Co., Fort Point, Cape Jellison, Stockton Springs, *R 150b.*

CHECKLIST OF THE ALPINE FLORA OF WESTERN BROOK POND AND DEER POND AREAS, GROS MORNE NATIONAL PARK

ALEXANDER ROBERTSON[1] AND B. A. ROBERTS[2]

ABSTRACT

This checklist provides a field list of the alpine and coastal plain flora of Western Brook Pond and Deer Pond areas in Gros Morne National Park, western Newfoundland. Plants are listed under six major habitat types; including coastal forest, tuckamore, barrens, peatlands, alpine meadow and rocks, cliffs and gullies. A general vegetation profile with main soil types is also given.

RÉSUMÉ

Cette liste de contrôle fournit un répertoire des flores alpine et de la plaine cotière de Western Brook Pond et Deer Pond á l'interieur du Parc National Gros Morne dans la région ouest de Terre-Neuve. Les plantes y sont énumérees selon les six principaux types d'habitat: la forêt côtière, les tuckamores, les terres stériles, les tourbiéres, les plaines alpines et les rochers, falaises et ravins. Une description générale de la végétation, incluant les principaux types de sol, y est aussi donnée.

This checklist is a result of frequent botanical excursions during the past decade to the Long Range Mountains, including two major backpacking expeditions in 1973 and 1976 (Robertson, 1977). The main study areas for the checklist are Western Brook Pond and Deer Pond in Gros Morne National Park.

While many species in the list have been recorded by a number of authors (Waghorne, 1890 94; Fernald, 1911; Rouleau, 1956; Damman, 1965; Bouchard, et al., 1978) only Fernald (1924–26) and Bouchard and Hay (1976) give detailed ecological information of the area, and their studies were primariliy limited to the coastal plain vegetation. Conversely our own studies over the past decade or so have concentrated on the inaccessible plateau summits and inland valleys of the Long Range Mountains in the Gros Morne National Park area.

This field checklist is designed for ready comparison of species in relation to types. Each habitat reflects the structure of vegetation in relation to geomorphology, soils and drainage.

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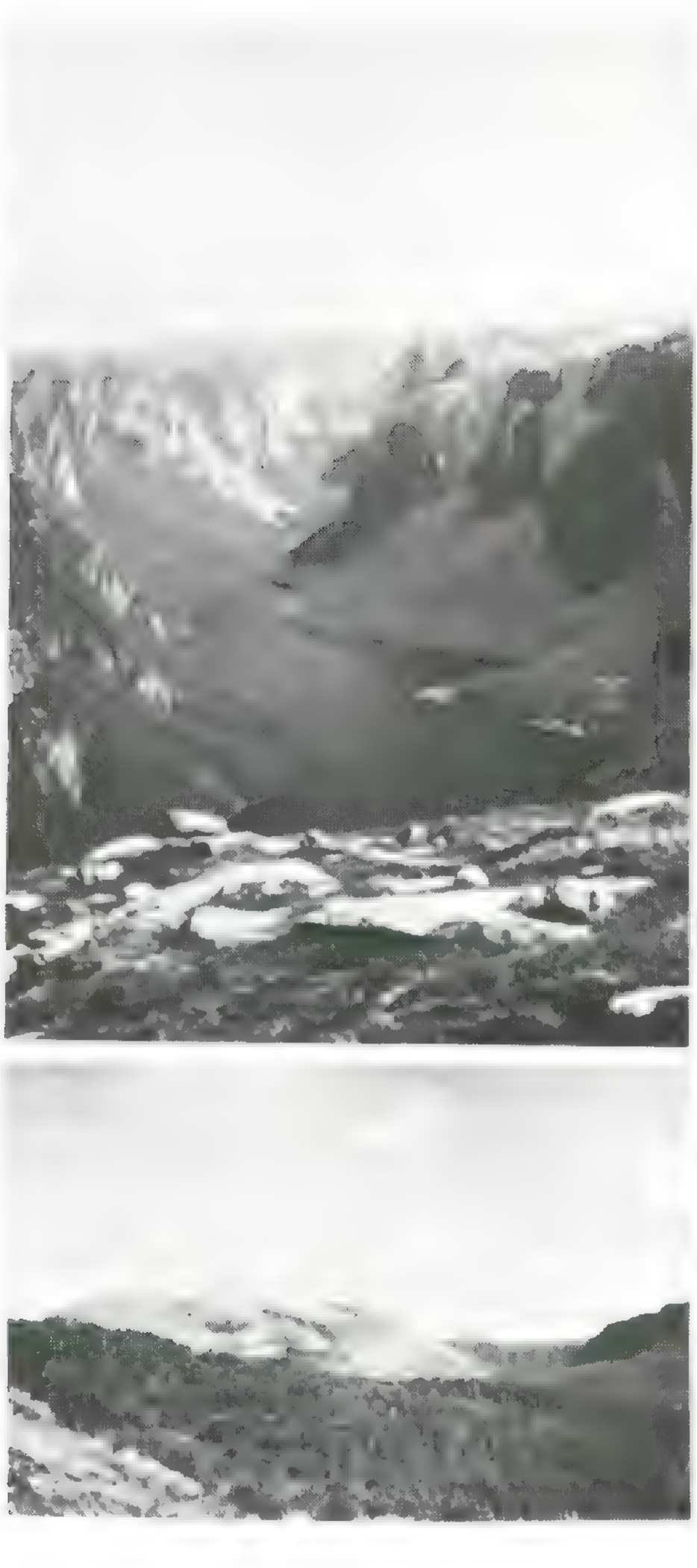


The canyon of Western Brook Pond was formed by glaciation. It is 27 km long and flanked on both sides by vertical cliffs rising 700 m to the plateau summits for almost its entire length. The gently rolling plateaux have a tundra vegetation mosaic of heath, slope fens, and tuckamore, interspersed with numerous small ponds in the valleys and exposed ridges of bedrock strewn with large erratic boulders. Fields of felsenmeers are quite common on the plateaux. Deer Pond is 20 km long and it is flanked by 500 m cliffs on its north side and steep forested slopes of Gros Morne on its south side. Figures 1 and 2 illustrate the vegetation of the summit plateaux and inland valleys of the area.

The Long Range Mountain system is an uplifted block of Grenville basement rocks of the Precambrian. These consist mainly

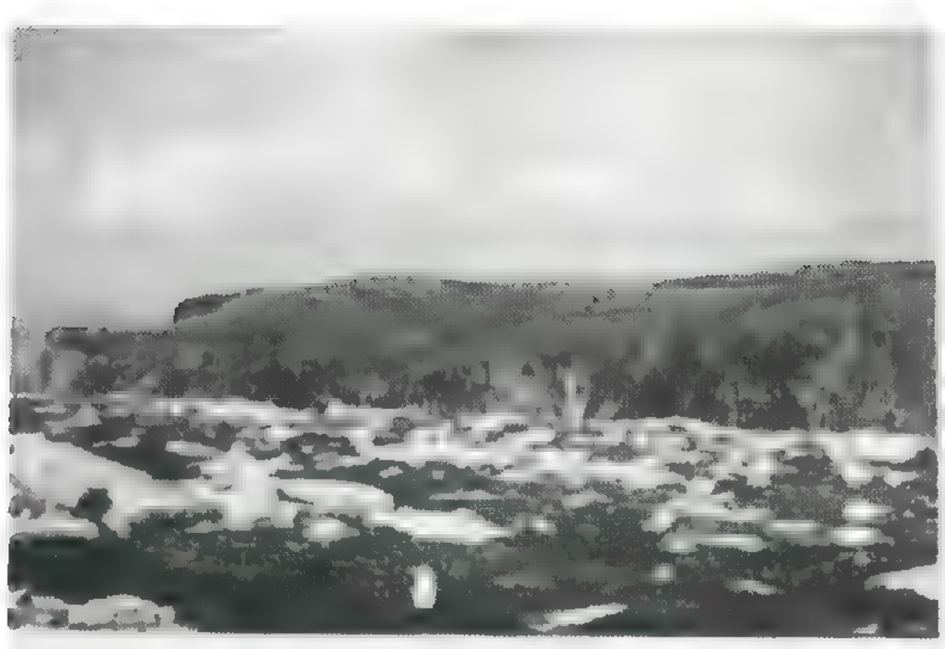
of metamorphic and igneous granite and granite gneiss. The cliffs of Western Brook Pond and Deer Pond are exposures of interbedded limestone, dolomitic slate, and quartzite, thrust upward along the major tectonic fault which separates the coastal plain from the Long Range plateau mountains. The plateau summits are capped by quartzite (Cummings, 1973).

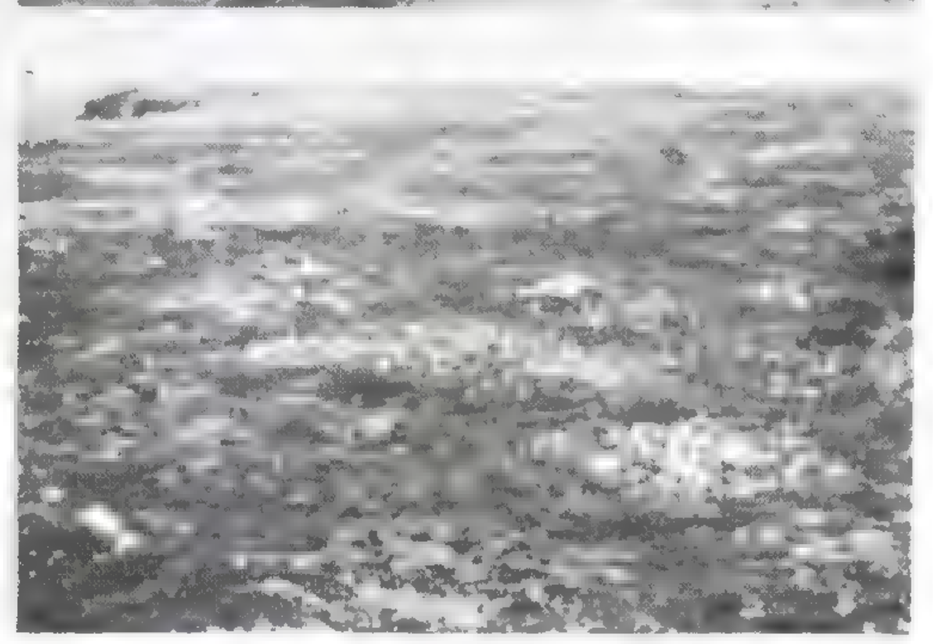
The checklist enumerates 250 taxa and its purpose is to provide a field list of vascular plants, principally the mountain flora. Of particular interest to us were the special varieties rarely seen by botanists. For instance, the inconspicuous *Euphrasia randii* forma *iodantha* is quite rare and our particular find appears more related to *E. confusa* of Europe than to our native *E. randii* complex. In the euminerotrophic slope fens at the eastern end of both Western Brook Pond and Deer Pond two distinct types of pitcher plant—*Sarracenia purpurea* forma *heterophylla* and *S. p.* var. *venosa*—grow abundantly together. On the barren plateau summits large snowfields remain throughout the year. On the perimeter of several snowfields in 1976 *Rubus acaulis, Phyllodoce coerulea, Pinguicula vulgaris,* and *Viola incognita* had barely reached anthesis stage in the beginning of September, while a mere 50 m away fruits on the same species had ripened much earlier in the season.

Six habitat types have been distinguished. Figure 3 gives a general profile of these zones. The following is a synopsis of each zone.

COASTAL FOREST (CF)

The coastal forest occupies the coastal plain and the lower slopes of the mountains. It is a complex mosaic of mesotrophic bogs, marshes, poor forests, and ponds with rocky shores. On the coastal plain the drier sites are forested by *Abies balsamea,* with a strong introgression of *A.* × *phanerolepis.* The wetter sites are characterized by *Picea mariana* forested fens. On the lower mountain slopes there is a higher component of *Betula papyrifera* in the predominantly *Abies balsamea* forest. Although the coastal forest is not strictly alpine, its flora has a high proportion of plants common to both lower and higher altitudes. Also, to gain access to the mountains on foot, travellers must pass through the coastal forest. Therefore, for reference and comparison it is appropriate to include coastal forest plants in the checklist.



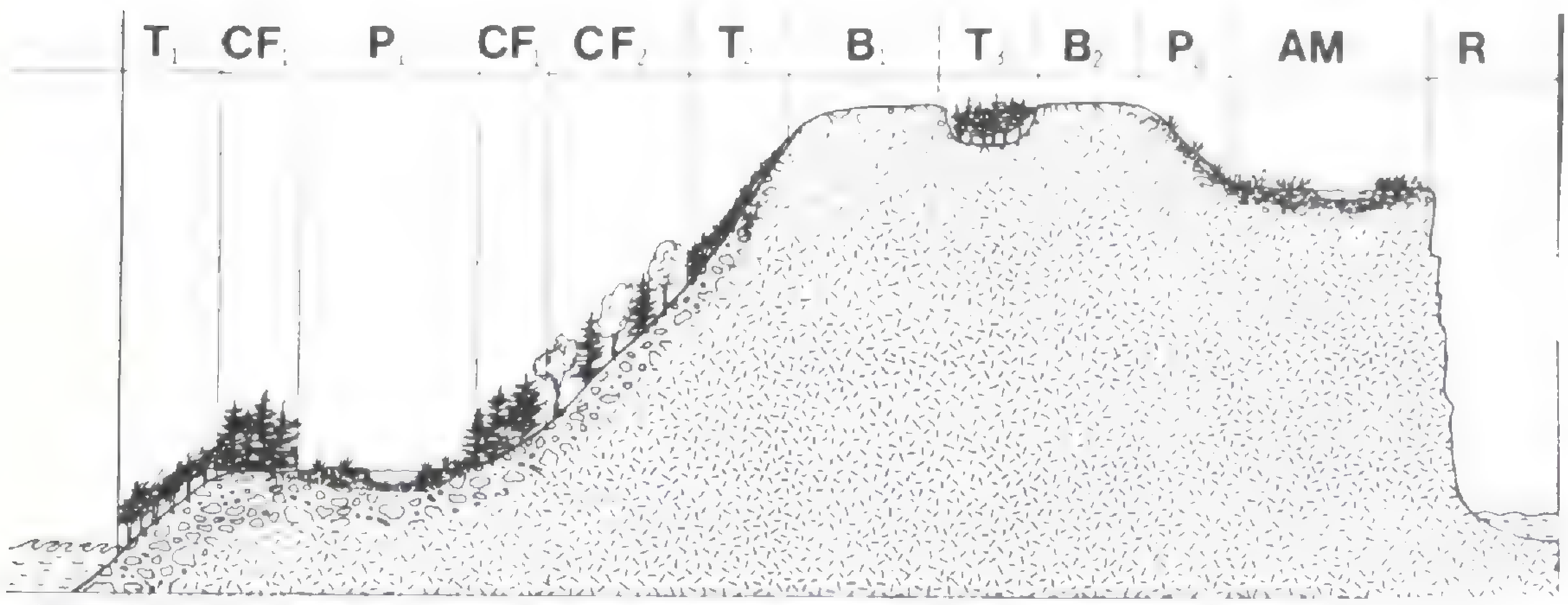


TUCKAMORE (T)

Plants occurring in the tuckamore (Krummholz) includes those found in *Abies* × *phanerolepis* tuckamore which dominates the exposed sea cliffs, and those of the mountain tuckamore. The mountain tuckamore has three variations namely, *A. balsamea, Picea glauca,* and *P. mariana. Abies balsamea* tuckamore is generally restricted to the dry rocky sites in sheltered depressions on the plateau summits; the average height is about 2 3 m. *Picea glauca* tuckamore occurs on gravelly soils of the exposed bluffs and mountain slopes; it varies from low scrub 1 1.5 m high to dense carpets 10 cm high. *Picea mariana* tuckamore dominates wet mucky soils in valleys and seepage slopes and varies from 1.5 4 m in height.

BARRENS (B)

The barrens are characterized by heath communities on dry gravelly soils. The heaths vary from carpets of *Empetrum nigrum*, containing Arctic-alpine plants (*Arctostaphylos alpina, Diapensia lapponica, Phyllodoce caerulea*), to broadleaf scrub (*Betula minor, B. glandulosa, Sorbus decora*). On exposed seepage slopes the shallow peaty soils form the rooting medium for dwarf shrubs such as *Vaccinium angustifolium, Potentilla fruticosa, Myrica gale, Salix vestita* var. *mensalis, S. cordifolia* var. *callicarpaea, Alnus crispa* forma *stragula, Nemophanthuus mucronata,* and for herbs (*Lycopodium lucidulum, Deschampsia flexuosa, Solidago macrophylla* var. *thyrsoidea, Maianthemum canadense, Cornus canadense*). *Osmunda regalis* var. *nana* covers extensive areas of moist, well-drained regosols on the northern aspects of mountain slopes.



Habitat Unit	Geomorphology	Soils*	Vegetation
CF	CF_1, ridged beach lines, some sections washed and reworked by marine action. CF_2, hummocky moraine, kettled.	CF_1, orthic ferro humic podzol. CF_2, gleyed humo ferric podzol to lithic humo ferric podzol on thin till areas.	CF_1, coastal forest dominated by Abies balsamea. CF_2, coastal forest dominated by Abies balsamea but having a higher component of Betula papyrifera.
T	T_1, ridged beach lines, some sections washed and reworked by moraine action. T_2, veneer moraine, occasional hummocky moraine.	T_1, orthic ferro humic podzols + ortstein. T_2, lithic humo ferric podzol.	T_1, Abies x phanerolepis tuckamore. T_2, Picea glauca tuckamore. T_3 Abies balsamea tuckamore.
B	B, veneer moraine, occasionally exposed bedrock. + seepage.	Lithic regosols, occasionally gleyed regosols or typic folisol.	B_1, arctic alpine barrens. B_2, exposed seepage slope barrens.
P	P_1, low plateau bogs, P_2, slope fens with seepage, shallow to intermediate in peat depth.	P_1, mesic fibrisol, P_2, typic mesisol sometimes very shallow.	P_1, low plateau bogs. P_2, shallow slope fens with seepage.
AM	Colluvium, pattern ground interspersed by slope fens.	Orthic to gleyed regosols + lithic, typic mesisols on slope fens.	Alpine meadows on gentle slopes.
R	Exposed bedrock, some scree and talus.	Lithic regosols and exposed bedrock.	Dwarf shrub and peaty ledges. Exposed bedrock devoid of vegetation.

*Soils are classified according to the Canadian System of Soil Classification proposed by the Canada Soil Survey Committee (1978).

PEATLANDS (P)

There are few sphagnaceous bogs on the higher elevations. The peatland plants in the checklist are generally those found on slope fens. Slope fens are shallow minerotrophic peats, influenced by nutrient-deficient seepage moisture derived from rather impervious granites and quartzite, characterized by a vegetation associated with poor soil (i.e. *Scirpus cespitosus* and *Drosera rotundifolia*). Sedimentation and cryoturbation are also important factors and these permit conditions for a wider diversity of species, for example *Pinguicula vulgaris, Glyceria borealis, Carex atratiformis, C. scirpoidea, Sanguisorba canadensis, Pyrus melanocarpa, Viola pallens,* and *Triadenum virginicum*).

ALPINE MEADOWS (AM)

The alpine meadows are common on the gentle slopes of sheltered valleys. They are rich with grasses (*Calamagrostis canadensis, Festuca rubra, Poa pratensis,* and *Sieglingia decumbens*), and herbs (*Habenaria dilatata, H. blephariglottis, Solidago purshii,* and *Sanguisorba canadensis*). *Myrica gale, Andromeda glaucophylla, Rhododendron canadense,* and *Chamaedaphne calyculata* are the dominant shrubs.

ROCKS, CLIFFS AND STEEP GULLIES (R)

This zone includes the cliffs that flank Western Brook Pond and Deer Pond and the steep gullies between them. The soils are mainly unstable rubbles on the scree slopes and more stabilized moist regosols on the ledges. Some of the rarer plants occur on the moist turfy soils of narrow ledges and crevices of these high cliffs; for example, *Ranunculus pedatifidus* var. *leiocarpus, Epilobium alpinum, Arctostaphylos uva-ursi* var. *coactilis.* Most of the wider ledges have dwarf shrub and scrub communities similar to those found on the barrens except that, presumably because of the drier conditions, *Kalmia angustifolia* and *Vaccinium angustifolium* are much more predominant. On peaty ledges *Carex scirpoidea, Prenanthes trifoliata* var. *nana, Solidago multiradiata, Drosera rotundifolia, Pinguicula vulgaris,* and *Potentilla tridentata* are the main constituents. *Taraxacum lapponicum, Hieracium groenlandicum, Leontodon autumnalis, Streptopus roseus,* and *Coniosel-*

inum chinensis can also be found at altitudes of 650 700 m near the rim of the cliffs along Western Brook Pond; no doubt their highest occurence in Newfoundland.

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CHECKLIST OF THE ALPINE FLORA OF WESTERN BROOK POND AND DEER POND AREAS, GROS MORNE NATIONAL PARK, NEWFOUNDLAND

Taxa	Habitat Types				
	CF	T	B	P	AM	R
EQUISETACEAE						
Equisetum Arvense L.		X				
E. sylvaticum L.		X				
E. palustre L.		X		X	X	
E. fluviatile L.		X			X	
LYCOPODIACEAE						
Lycopodium selago (L.) Bernh. var. *appressum* Desv.			X	X		
L. lucidulum Michx.		X	X			
L. complanatum L.		X				
L. annotinum L.		X				
L. annotinum var. *pungens* (La Pylaie) Desv.				X		X
L. obscurum L.		X	X			
L. inundatum L.				X	X	
SELAGINELLACEAE						
Selaginella selaginoides (L.) Link.					X	X
OSMUNDACEAE						
Osmunda regalis L. var. *nana* Fern			X		X	X
O. cinnamomea L.	X	X				
POLYPODIACEAE						
Cystopteris fragilis (L.) Bernh.						X
Onoclea sensibilis L.	X					
Dryopteris disjuncta (Ledeb) C. V. Mort.	X	X				
D. phegopteris (L.) Christens.						X
D. spinulosa (O. F. Mueller) Watt var *intermedia* (Muhl.) Underw.	X	X			X	
Polystichum Braunii (Spenner) Fée var. *purshii* Fern.	X					X
TAXACEAE						
Taxus canadensis Marsh	X	X				
PINACEAE						
Larix laricina (Du Roi) K. Koch	X	X		X	X	
L. laricina forma *depressa* Rousseau			X	X		
Picea glauca (Moench) Voss forma *parva* (Vict.) Fern. & Weath.					X	
Picea mariana (Mill.) B.S.P.	X					
P. mariana forma *semiprostrata* (Peck) Blake					X	
Abies balsamea (L.) Mill.	X	X				

Taxa	Habitat Types					
	CF	T	B	P	AM	R
A. balsamea forma *hudsonia* (Jacques) Fern. & Weath.		X				
A. × *phanerolepis* (Fern.) Liu	X	X				
Juniperus horizontalis Moench			X			
J. communis var. *depressa* Pursh			X		X	X
SPARGANIACEAE						
Sparganium angustifolium Michx.	X				X	
Sparganium minimum (Hartm.) Fries					X	
ZOSTERACEAE						
Potamogeton natans L.	X			X	X	
P. gramineus L.					X	
P. oakesianus Robbins	X			X	X	
GRAMINEAE						
Festuca rubra L.	X	X			X	X
Glyceria canadensis (Michx.) Trip.	X	X	X	X	X	X
G. borealis (Nash) Batchelder			X	X		
G. striata (Lam.) Hitchc.						X
Poa palustris L.		X		X		
P. pratensis L.	X				X	X
Sięglingia decumbens (L.) Bernh.					X	
Agrostis alba L.			X			X
A. scabra Willd.	X	X				
Calamagrostis canadensis (Michx.) Nutt.	X	X		X	X	X
Deschampsia flexuosa (L.) Trin.	X	X	X			X
Anthoxanthum odorantum L.	X					
CYPERACEAE						
Eriophorum angustifolium Honckeny	X	X		X		
E. spissum Fern.	X			X		
E. chamissonis C. A. Mey	X			X		
E. viridi-carinatum (Engelm.) Fern.			X	X		
E. virginicum L.				X		
Rhynchospora alba (L.) Vahl.		X				
Scirpus cespitosus var. *callosus* Bigel.	X	X	X	X	X	X
Carex stipita Muhl.	X					X
C. disperma Dew.	X	X				X
C. trisperma Dew.	X	X				
C. canescens L.	X					
C. brunnescens (Pers.) Poir	X	X				
C. brunnescens var. *sphaerostachya* (Tuck.) Kuk.	X	X				X
C. exilis Dew.				X	X	
C. sterilis Willd.						X
C. angustior Mack.	X	X		X		
C. muricata L.		X				

Taxa	Habitat Types					
	CF	T	B	P	AM	R
C. scoparia Schkuhr	X					X
C. projecta Mack.	X	X				
C. aquatilis Wahlenb.	X				X	
C. nigra (L.) Reichard				X	X	
C. nigra var. *strictiformis* (Bailey) Fern.				X	X	
C. stylosa C. A. Meyer				X		
C. atratiformis Britt.	X					
C. bauxbaumii Wahlenb.	X				X	
C. livida (Wahlenb.) Willd.	X			X	X	
C. vaginata Tausch.	X					
C. flava L.	X					
C. viridula Michx.	X					
C. michauxiana Boeckl.	X					
C. folliculata L.	X					
C. intumescens Rudge	X					
C. oligosperma Michx.					X	
C. paupercula Michx. var. *irrigua* (Wahlenb.) Fern.				X		
C. saxatilis L. var. *miliaris* (Michx.) Bailey						X
JUNCACEAE						
Juncus trifidus L.			X			
J. filiformis L.		X			X	
J. effusus L.	X					
J. articulatus L.	X					
Luzula spicata (L.) DC.			X		X	
L. multiflora (Retz.) Lejeune var. *fusconigra* Celak			X		X	
LILIACEAE						
Tofieldia glutinosa (Michx.) Pers.				X		
Clintonia borealis (Ait.) Raf.	X	X			X	
Smilacina racemosa (L.) Desf.	X	X				X
S. stellata (L.) Desf.	X					X
S. trifoliata (L.) Desf.		X				
Maianthemum canadense Desf.	X	X	X	X	X	X
Streptopus amplexifolius (L.) DC.	X					
S. amplexifolius var. *oreopolus* (Fern.) Fassett		X				
S. roseus Michx.	X	X				X
ORCHIDACEAE						
Habenaria dilatata (Pursh.) Hooker	X			X	X	
H. hyperborea (L.) R. Br.	X	X				
H. blephariglottis (Willd.) Hooker				X	X	
H. clavellata var. *ophioglossum* Fern.					X	
Goodyera repens (L.) R. Br.	X	X				
Malaxis uniflora Michx.	X	X			X	

Taxa	Habitat Types					
	CF	T	B	P	AM	R
SALICACEAE						
Salix discolor Muhl.	X	X			X	X
S. vestita Pursh var. *mensalis* Fern.			X			
S. lucida Muhl.	X	X				
S. uva-ursi Pursh			X			
S. cordifolia Pursh var. *callicarpaea* (Trautv.) Fern.			X			
S. rigida Muhl.	X				X	
S. glaucophylloides Fern.	X					
S. bebbiana Sang.	X	X				
Populus tremuloides Michx.	X	X				
MYRICACEAE						
Myrica gale L.	X	X			X	
M. gale var. *subglabra* (Chev.) Fern.				X	X	X
CORYLACEAE						
Betula papyrifera Marsh.	X				X	X
B. papyrifera var. *cordifolia* (Regel.) Fern.	X	X				
B. minor (Tuckerm.) Fern.			X		X	
B. glandulosa Michx.			X			
B. pumila L. var. *renifolia* Fern.			X	X	X	
B. michauxii Spach.			X	X	X	
Alnus crispa (Ait.) Pursh forma *stragula* Fern.			X			X
A. rugosa (Du Roi) Spreng.	X	X			X	
URTICACEAE						
Urtica gracilis Ait.	X					
SANTALACEAE						
Geocaulon lividum (Richards) Fern.	X	X				
NYMPHAEACEAE						
Nyphar variegatum Engelm.	X				X	
RANUNCULACEAE						
Ranunculus acris L.	X					X
R. flammula L.	X	X				
R. reptans L.	X				X	
R. aborvitus L. var. *acrolasius* Fern.	X	X				
R. pedatifidus J. E. Smith var. *leiocarpus* (Trautv.) Fern.		X	X			X
R. repens L.	X	X				
Thalictrum alpinum L.	X				X	X
T. polygamum Muhl.	X				X	
Coptis groenlandica (Oeder) Fern.	X	X				
Actaea rubra (Ait.) Willd.	X	X				

Taxa	Habitat Types					
	CF	T	B	P	AM	R
SARRACENIACEAE						
Sarracenia purpurea L.				X	X	
S. purpurea forma *heterophylla* (Eat.) Fern.				X	X	
S. purpurea var. *venosa* (Raf.) Fern.				X	X	
DROSERACEAE						
Drosera rotundifolia L. forma *breviscapa* (Regel) Domin	X			X	X	X
D. intermedia Hayne				X	X	
SAXIFRAGACEAE						
Saxifraga aizoon Jacq. var. *neogaea* Butters	X					
Mitella nuda L.	X	X				X
Ribes lacustre (Pers.) Poir	X					
R. glandulosum Grauer.	X	X				X
R. triste Pall		X				X
ROSACEAE						
Spirea latifolia (Ait.) Borkh.	X	X				
S. latifolia var. *spetentrionalis* Fern.		X			X	X
Sorbus americana (March) DC.	X					X
S. decora (Sarg.) Schnied. var. *groenlandica* (Schneid.) Fern.		X	X		X	X
S. melanocarpa (Michx.) Willd.		X		X	X	X
Amelanchier bartramiana (Tausch) Roemer	X	X			X	X
A. laevis Wieg.	X	X			X	X
Potentilla fruticosa L.	X	X			X	X
P. fruticosa var. *tenuifolia* Lehm.			X	X		
P. tridentata Ait.			X			X
P. norvegica L.	X					
Geum rivale L.	X	X				
Rubus pubescens Raf.	X	X			X	X
R. chamaemorus L.			X	X	X	
R. acaulis Michx.		X			X	
Sanguisorba canadensis L.	X		X		X	X
Prunus pensylvanica L. fil.	X	X				X
LEGUMINOSAE						
Trifolium repens L.	X					
T. pratense L.	X					
Vicia cracca L.	X	X				
AQUIFOLIACEAE						
Nemopanthus mucronatus (L.) Trel.	X	X	X		X	X

Taxa	Habitat Types					
	CF	T	B	P	AM	R
EMPETRACEAE						
Empetrum nigrum L.			X			X
E. nigrum var. *purpureum* (Raf.) Fern.			X			
ACERACEAE						
Acer spicatum Lam.	X					X
A. rubrum L.	X					
Rhamnaceae						
Rhamnus alnifolia L'Her.		X				
GUTTIFERAE						
Triadenum virginicum L.				X	X	
VIOLACEAE						
Viola cucullata Ait.	X					X
V. incognita Brainerd	X	X				
V. pallens (Banks) Brainerd	X	X		X	X	
ONAGRACEAE						
Epilobium angustifolium L.	X	X				X
E. alpinum L.	X					X
E. palustre L. var. *oliganthum* (Michx.) Fern.	X				X	
Oenothera biennis L.	X					
Circaea alpina L.		X				
ARALIACEAE						
Aralia nudicaulis L.	X	X				
UMBELLIFERAE						
Conioselinum chinensis (L.)	X					X
Heracleum maximum Bartr.	X					
CORNACEAE						
Cornus canadensis L.	X	X			X	X
C. suecica L.			X	X		
C. stolonifera Michx.	X	X			X	
PYROLACEAE						
Moneses uniflora L.	X	X				
Pyrola secunda L.	X					
P. rotundifolia L.			X	X		
Monotropa uniflora L.		X				
ERICACEAE						
Rhododendron canadense (L.) Torr.	X	X			X	
Kalmia latifolia L.	X				X	
K. polifolia Wang.				X	X	

Taxa	Habitat Types					
	CF	T	B	P	AM	R
Phyllodoce caerulea (L.) Bab.			X			X
Andromeda glaucophylla Link.				X	X	
Chamaedaphne calyculata L.				X	X	
C. calyculata var. *latifolia* (Ait.) Fern.			X			
Epigaea repens L.	X					
Gaultheria procumbens L.	X					
G. hispidula (L.) Bigel.		X				X
Loiseleuria procumbens (L.) Desv.			X			
Arctostaphylos uva-ursi (L.) Spreng var. *coactilis* Fern. & Macbr.			X			X
A. alpina (L.) Spreng.			X			X
Gaylussaccia dumosa (Andrews) Torrey & Gray var. *Bigeloviana* Fern.				X		
G. baccata (Wang.) K. Koch.	X	X				
Vaccinium uliginosum L.			X			X
V. cespitosum Michx.			X			X
V. angustifolium Ait.			X			X
V. vitis-idaea L.			X			X
V. oxycoccus L.				X	X	
V. macrocarpon Ait.				X		
DIAPENSIACEAE						
Diapensia lapponica L.			X			X
PRIMULACEAE						
Trientalis borealis L.	X	X				
Primula mistassinica Michx.	X					
P. laurentiana Fern.	X					
SCROPHULARIACEAE						
Euphrasia randii Robins. forma *iodantha* (Fern. & Wieg.) Fern.			X			
E. americana Wettst.	X					
Rhinanthus crista-galli L.	X					
Pedicularis palustris L.	X					
LENTIBULARIACEAE						
Utricularia minor L.	X			X	X	
U. intermedia Hayne	X					
Pinguicula vulgaris L.					X	X
CAPRIFOLIACEAE						
Lonicera villosa (Michx.) Roemer & Schultes var. *calvescens* (Fern. & Wieg.) Fern.						X
Linnaea borealis L.		X				
Viburnum cassinoides L.		X				X

Taxa	Habitat Types					
	CF	T	B	P	AM	R
V. trilobum Marsh.	X	X			X	
CAMPANULACEAE						
Campanula rotundifolia L.	X					X
Lobelia dortmanna L.	X				X	
COMPOSITAE						
Eupatorium maculatum L	X					
Solidago macrophylla Pursh var. *thyrsoidea* (Mey.) Fern.		X	X			
S. canadensis L.	X					
S. uliginosa var. *terra-novae* (T. & G.) Fern.		X	X			
S. multiradiata Ait.						X
S. purshii Porter				X	X	
S. lepida De Candolle var. *fallax* Fern.		X				
Aster novae-angliae L.	X					
A. puniceus var. *oligocephalus* Fern.			X			
A. radula Ait.				X		
A. umbellatus Miller forma *flexicaulis* (House) Fern.	X					
Achillea millefolium L.	X					X
Senecio pauperculus Michx.	X					
Cirsium arvense (L.) Scop.	X	X				
C. muticum Michx.	X	X				
Leontodon autumnalis	X					X
Taraxacum lapponicum Kilhm.	X					X
T. officinalis Weber.	X					
Prenanthes trifoliolata (Cossini) Fern. var. *nana* (Bigel.) Fern.		X	X			X
Hieracium groenlandicum Arv.-Touv.						X
H. kalmii L.						X

NESTING OF BEETLES AND ANTS IN *CLIBADIUM MICROCEPHALUM* S. F. BLAKE (COMPOSITAE, HELIANTHEAE)

GUY L. NESOM AND TOD F. STUESSY

In the course of a systematic study of the genus *Clibadium* (Compositae, Heliantheae), the junior author noticed that portions of the stems, including nodal regions, of *C. microcephalum* S. F. Blake sometimes are hollow, somewhat swollen, and split open. Of 12 available herbarium collections, four showed this condition in varying degrees (see especially *King 6560;* not seen, however, in the type specimen, *Hitchcock 21873*).

Clibadium microcephalum, a shrub 1–2 meters tall, is known only from Ecuador, where it grows in tropical vegetation at 800–1400 m on the eastern side of the Andes. Field studies in Ecuador in September, 1979, offered the opportunity to answer the following questions: (1) what is the cause of the stem cavities; (2) are these apparent abnormalities in stem growth restricted to *Clibadium microcephalum* within the genus; and (3) are the cavities found in plants of other genera in the same geographical area?

MATERIALS AND METHODS

On September 1, 1979, three populations of *Clibadium microcephalum* were studied. All were in disturbed tropical vegetation along the Baños-Puyo road at ca. 1300 m, Tungurahua, Ecuador. The exact locations are: *Stuessy & Nesom 5814, 5822,* and *5823,* respectively 2.8, 4.8, and 3.3 kms E of Río Topo. In each population, composed of 10–20 closely spaced individuals, 50 stems with cavities were opened and examined for structure and contents. Normal-appearing stems were also inspected for comparison. Colonized and uncolonized stems were preserved dry and in FAA. At each locality searches were made for plants of any taxonomic group which might show similar swellings and cavities. Vouchers of plants discussed are deposited in the Ohio State University Herbarium (os). Collections of insects involved in this aspect of the biology of *Clibadium microcephalum* were also made, and these have been deposited in the Ohio State University Collection of Insects and Spiders and in the Los Angeles County Museum.

RESULTS

Stems of *Clibadium microcephalum* in which cavities are formed normally are 3–8 mm diam (Fig. 1) of which 2/3–3/4 of the area is pith. There are no naturally formed internal chambers. Round to narrowly elliptic lenticels (ca. 1 mm diam) are common on stems of some plants (Fig. 2). On some plants small, spherical protuberances, apparently outgrowths of the epidermis but not extra-floral nectaries or food bodies, are formed in abundance, but they were not observed to be eaten or to be the object of attention of any of the insects on the plants. Nor was there any evidence of leaf predation on inhabited or uninhabited plants of *C. microcephalum*.

The cavities are formed initially by activities of the beetle, *Scolytodes elongatus* Schedl. Adults which are 3–4 mm long, and 1–1.5 mm wide, apparently enter the stems through a lenticel in the internodal regions or sometimes through a leaf scar at the nodes, widening an orifice until it can be recognized as a conspicuous entrance into the cavity (Fig. 2). The chamber formed as the beetle excavates its way into the pith then serves as a brood chamber, since eggs and numerous larvae were almost always found where adults were present. Chambers (Fig. 3) ranged from 1 to ca. 20 cm long, and each housed 2–8 adults; the beetles were always at one end of the chamber adjacent to a section of intact pith. The entrance hole may also serve as an exit, since in many cases only a single opening could be found in occupied and unoccupied chambers. Larvae noticeably larger than those typically associated with the adult beetles (presumably another insect species) were occasionally found, especially in cavities in nodal regions.

Three species of ants were discovered in the cavities initially formed by the beetles. The two species, *Pachycondyla unidentata* Mayr and *Pseudomyrma* sp., were fairly common in stems of populations *5822* and *5823*, and one individual of *Pachycondyla unidentata* was found at population *5814*. These relatively large ants were always solitary, in short cavities, and eggs were infrequently found with the adults. In several plants of population *5814* large

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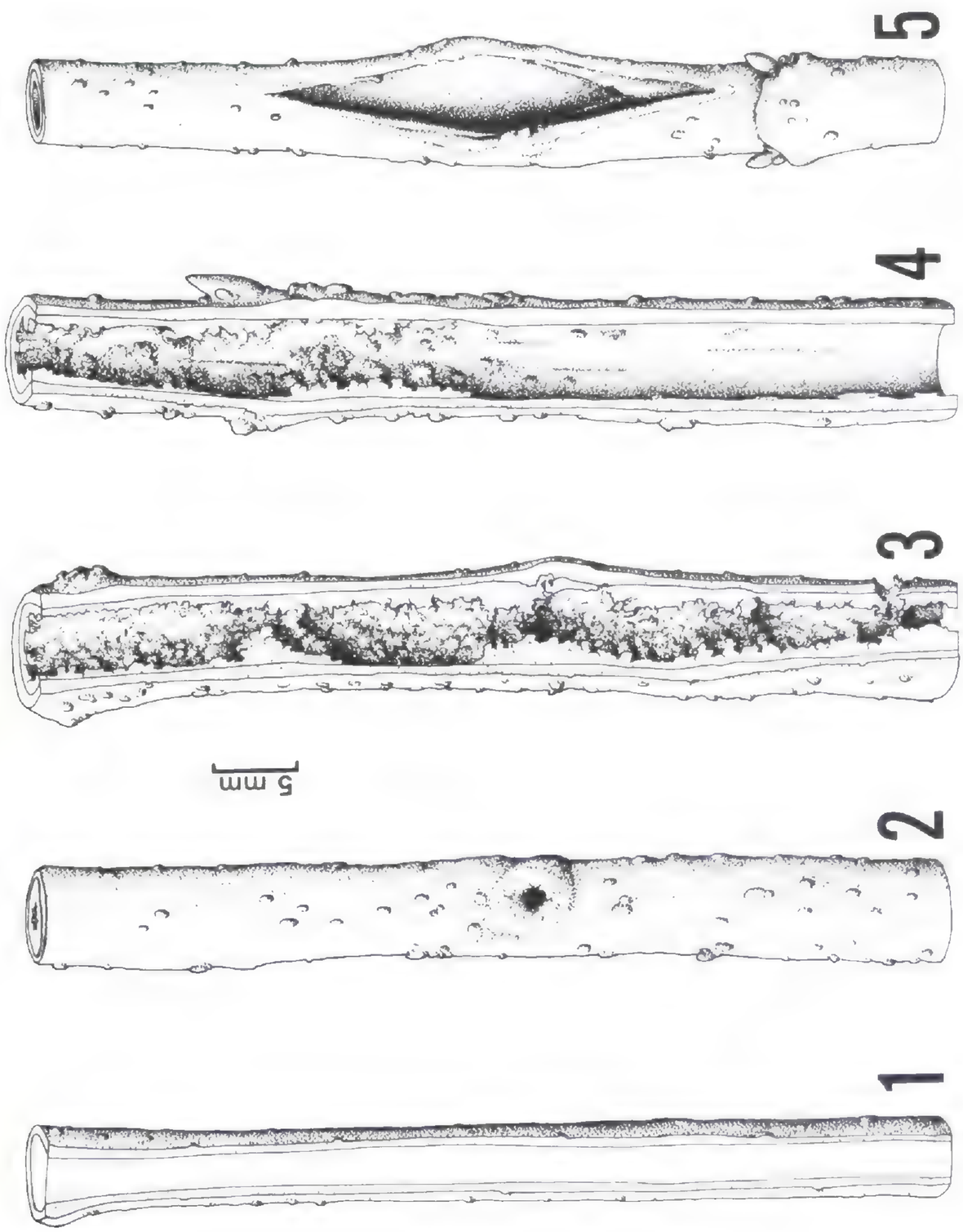
Figures 1–5. **Stems and stem cavities of Clibadium microcephalum** (all longitudinal sections except Fig. 2). **1,** intact pith; **2,** lenticels and entrance hole to inner caity; **3,** cavity with beetle frass and some traumatic tissue; **4,** portion of cavity cleaned by ants; **5,** opening with healed edges. All same scale.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colonies of the much smaller ant, *Myrmelachista* sp., were nesting in extensive cavities. Eggs, larvae, and a queen of this species were collected from one of the plants.

As the ants begin to utilize the beetle-formed excavations, they widen the cavities and remove the frass (Fig. 4) which is abundant when the beetles are in occupancy. Small amounts of traumatic tissue apparently are elaborated by the plants on the inner walls of the cavities, but there was no indication that ants use this as a food source. Bailey (1922) also reported such "house-cleaning" by ants in stems of *Cecropia angulata* I. W. Bailey. No fungi were found within the cavities, nor were coccids, common in many myrmecophytes (Ule, 1906), in evidence.

The colonized portions of the stems may continue to grow slightly in circumference relative to the uncolonized sections. The nodal regions, particularly, may appear gall-like and become 5-12 mm wide. Several very long chambers, up to 30 cm long, were found unoccupied. Stems very often split and form a broad opening which reveals the chamber within (Fig. 5); continued cambial activity appears to heal the edges of the split tissue. Stems do not appear to be seriously structurally weakened by this deformation.

At the three localities, seven species of ants were observed foraging on the leaves of *Clibadium microcephalum*. Of the three stem-inhabiting species only two individuals of *Pseudomyrma* sp. were found foraging (at population *5822*). Also, on plants of population *5822* another species of *Pseudomyrma* was foraging, and *Crematogaster nigropilosa* Mayr was feeding on several large, unidentified larvae which were attached to leaves. On plants of population *5823*, *Crematogaster nigropilosa*, *Camponotus* sp., and *Procryptocerus* sp. were foraging; *Procryptocerus* sp. was foraging at population *5814*. *Scolytodes elongatus* was not observed on plants outside of the cavities.

At the time the initial draft of this paper was written, it was believed that no other species of *Clibadium* in Ecuador or elsewhere had stem cavities which would suggest similar insect activity. In particular, the closely related *C. mexiae* S. F. Blake, which also grows in the same general region as *C. microcephalum* (both species found together at one location, 5 kms E of Mera, *Stuessy & Jansen 4967* and *4968*, respectively), is not known to have such cavities. However, four collections of *Clibadium arboreum* J. D. Smith from Guatemala (3) and Chiapas, Mexico (1) (respectively, *Contreras*

6264, LL; *Poll 70,* US; *White 5424,* OS; *Breedlove 10145,* NY) subsequently were found that also had swollen stems with cavities. One adult beetle was found in one collection (*Breedlove 10145*), and it is the same species of *Scolytodes* (C. Triplehorn, pers. comm.) found in Ecuador in *C. microcephalum.* Although the two species of *Clibadium* had not before been regarded as particularly closely related, due principally to the wide geographic separation, an examination of floral and vegetative features reveals no significant differences. Further studies need to be done on the relationships of these two taxa, but it is obvious that they are very closely allied, if not even conspecific. The stem deformation caused by the *Scolytodes* beetle provided an important clue to this close relationship.

In addition to growing in the valley of the Río Pastaza where the field studies were conducted, *C. microcephalum* is also known from the valley of the Río Paute (ca. 140 kms S, near Mendez). One of the two collections from this region, *Camp E-1484,* shows swollen nodes of the stems, but it is not known if *Scolytodes* or some other factors are responsible for the enlargement.

Searches at the *Clibadium* localities revealed only one other unidentified, sterile shrub (at population *5822*) which showed enlarged stems with excavations inside. No live organisms were found in these cavities, but pupa cases were present which were considerably larger than expected for *Scolytodes elongatus.* These may have been the same as the large, unidentified larvae occurring occasionally in the nodal regions of *Clibadium microcephalum.*

DISCUSSION

The situation reported here appears to fall at one extreme of an array of insect-plant relationships which vary from mutualism to commensalism. In "true" myrmecophytes, such as *Acacia* of Latin America (Janzen, 1966), *Cecropia* (Janzen, 1969; Downhower, 1975), *Cordia nodosa* (Bailey, 1924) and *Duroia saccifera* (Spruce, 1908), the plants offer ants nutrition and preformed, hollow, hypertrophic areas as domicile in return for protection from predation or competitive interaction with other plants. In some cases, the plants are dependent upon extra nutrients supplied by the ants in residence (Janzen, 1974). In *Clibadium microcephalum* the ants appear only to be utilizing a convenient living space originally formed by the scolytid beetles. For the beetles, the plants of this

particular species of *Clibadium* are anatomically and/or chemically attractive, furnishing both domicile and nutriment. However, there are no regularities in the placement of entrance or exit holes which might indicate special adaptations of the plants to accommodate the insects, nor are the cavities formed until the insects enter first. Neither is there any evidence of a mutualistic relationship between the beetles and plants.

The morphological features which result from the insect habitation on stems of *Clibadium microcephalum* occur with sufficient frequency to be used as supplementary taxonomic characters. Although the existence of the cavities on the shrubs is not revealed by every herbarium specimen (they are usually taken from the top part of the plant where the inforescences are produced), our observations in the three populations in Ecuador showed almost all plants with cavities somewhere on the stems. This species of *Clibadium* is distinct from its congeners in floral features, but the stem characteristics provide another specific differentium. The only other report of cauline ant inhabitants of plants in the Compositae is from *Erigeron maximus* (D. Don) DC. (Wheeler, 1942), a large, herbaceous species from Brazil.

The utilization by ants of stem cavities subsequent to their formation by beetles apparently is not common, but it is known from several examples in the African tropics and temperate regions (Wheeler, 1942). In none of the examples, including the one reported here, does there appear to be interaction between the beetles and any of the ants which follow them into their cauline accommodations. It is not known whether the ants in every case wait for empty chambers or whether they may force the beetles out. However, as evidenced by the abundance of empty, unoccupied chambers in the stems of *Clibadium microcephalum*, there is no lack of space for ant inhabitants.

This is apparently the first report of any species of *Pachycondyla* inhabiting stems. Species of *Pseudomyrma* and *Myrmelachista* have been observed as facultative inhabitants of stems or petioles (Wheeler, 1942), and a recent report describes the association of *Myrmelachista* sp. with a mealy bug and a small Costa Rican tree (Stout, 1979). The obligate relationships of *Pseudomyrma* spp. with *Acacia* plants are well known, but these ants will nest in preformed cavities in stems of other woody plants as well as in herbaceous dicots and grasses (Creighton, 1950).

The beetle inhabitant, *Scolytodes elongatus,* was originally described from Brazil (Schedl, 1935), where it was collected on *Mikania* sp. (Compositae). The few subsequent collections of this beetle have all been from Brazil (D. E. Bright, pers. comm.). Other scolytid beetles are known to burrow and breed in similar habitats—fruits, seeds, petioles, leaf midveins, and bark, as well as twigs and larger leaves (Browne, 1963; Beaver, 1979). Particularly, other species of *Scolytodes* have been observed in southern Mexico and Central America to burrow in the pith of the long petioles of *Cecropia* (Bright, pers. comm.). On the latter plants, as in *Clibadium microcephalum,* the chambers are sometimes utilized by ants as domatia after the beetles have gone. Bailey's observations on *Cecropia angulata* (1922) did not include a report of beetle habitation of the petioles. In many *Cecropia* species, there are preformed internodal cavities and thin areas in the stem wall, the prostomata, through which the mutualistic *Azteca* ants enter.

Most scolytid beetles have wide niche breadths, but Beaver (1979) has found that some species of tropical forests show niche separation largely through preference for different host plants. For example, *Corythylus columbianus* Hopkins, and four other beetles of the related family, Platypodidae, breed only in living trees and are relatively host-specific. Scolytids also have been reported to make galleries and live in large colonies in stems of *Phoradendron* (Schwarz, 1901). The *Scolytodes-Clibadium* association reported here is an addition to this accounting of host specialization.

ACKNOWLEDGMENTS

Special thanks go to: Donald E. Bright, Biosystematics Research Institute, Agriculture Canada, Ottawa, for identification of *Scolytodes elongatus* and information on its distribution; Roy R. Snelling, Department of Entomology, Los Angeles County Museum of Natural History, for identification of the ants; Charles A. Triplehorn of Ohio State University for general help with insect specimen examination and identification; David M. Dennis for drawing Figs. 1–5; the Graduate School of the Ohio State University for support of G.N. on a University Postdoctoral Fellowship; and the National Science Foundation for support to T.F.S. for field work under grant INT 76-84454.

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ADDITIONAL TAXONOMIC AND NOMENCLATURAL NOTES ON FERNS

ROLLA TRYON AND ALICE F. TRYON

Changes in the classification and related nomenclature have been made in several families for a new account of ferns and fern allies centering on tropical America (Tryon & Tryon, 1982, in press). The status of these in relation to the general classification will appear in this main work, but preliminary notice is made here and in an earlier paper (Rhodora **83:** 133–137, 1981). Research has been supported by National Science Foundation Grants DEB 7412317 and DEB-7803148.

1. The small central American species *Polypodium anetioides,* recognized as the monotypic genus *Hyalotrichopteris,* is characterized by unusual leaf trichomes with a protruding basal gland-cell and sori, with inconspicuous paraphyses, that are usually borne at the tip of a free vein but sometimes below the tip. These characters also occur in species inseparable from *Campyloneurum,* such as *C. occultum* and *C. trichiatum* (Rosenst.) Ching and the rather simple venation of *Hyalotrichopteris* is similar to that of small leaves of *Campyloneurum* species. The following new combinations are made in *Campyloneurum* and a new species with large leaves is described from Peru.

Campyloneurum anetioides (Christ) R. & A. Tryon, *comb. nov.* *Polypodium anetioides* Christ, Bull. Soc. Bot. Genève II, **1:** 219. 1909. *Hyalotrichia* Copel., Amer. Fern Jour. **42:** 12. 1953, not Dennis, 1949. *Hyalotrichopteris* W. H. Wagner, Taxon **27:** 548. 1978, *nom. nov.* for *Hyalotrichia* Copel.

Campyloneurum occultum (Christ) R. & A. Tryon, *comb. nov.* *Polypodium occultum* Christ, Bull. Herb. Boiss. II, **5:** 7. 1905.

Campyloneurum pascoense R. &. A. Tryon, *spec. nov.*

Lamina ad 1.9 m longa et ad 17 cm lata, coriacea, basi longe decurrenti, venis infra prominentibus, ad centrum inter venas primarias laterales areolis basalibus plerumque 4–7 venis liberis. HOLOTYPUS: Oxapampa, Dept. Junín, Peru, sent. 1944, *J. Soukup 2340* (GH, 3 sheets; F ex GH, 1 sheet). PARATYPUS: Oxapampa, Dept. Pasco, Peru, 1768 m, Augusto, 1947, *J. Soukup 3352* (GH, 2 sheets; US ex GH, 1 sheet).

Campyloneurum phyllitidis (L.) Presl and *C. tucumanense* (Hieron.) Ching, with leaves sometimes up to 1.5 m long, may be distinguished from *C. pascoense* by the following characters. The lamina is firmly papyraceous in *C. phyllitidis* and on the abaxial surface the veins are not or only slightly raised, and in the central portion of the lamina, the basal areolae between two primary lateral veins usually have 3-4 free veins. *Campyloneurum tucumanense* also usually has 3-4 free veins in the basal areolae, and the lamina is membranous to membranous-papyraceous and rather shortly decurrent at the base.

Each collection represents a complete lamina but only a portion of the petiole; there are no data on the labels aside from those cited. The 1947 collection was made after the Department of Pasco was established from part of the Department of Junín, on November 27, 1944.

2. *Monachosorum* Kze. is a small, Asiatic genus of uncertain affinity. It is treated as a monotypic tribe in the Dennstaedtiaceae on the basis of the chromosome reports $n = 56$ and 84 which are within the range of numbers known in the family, and the irregularly tuberculate spores which generally resemble those of some genera in the family.

Dennstaedtiaceae tribe **Monachosoreae** (Ching) R. & A. Tryon, *stat. nov.* Monachosoraceae Ching, Acta Phytotax. Sinica **16** (4): 17. 1978.

3. Several segregate genera are included in *Dryopteris*, among them *Phanerophlebiopsis* Ching. The type species is accordingly placed in *Dryopteris*.

Dryopteris Tsiangiana (Ching) R. &. A. Tryon, *comb. nov. Phanerophlebiopsis Tsiangiana* Ching, Acta Phytotax. Sinica **10:** 115. 1965.

4. Plants of *Lophosoria quadripinnata* (Gmel.) C. Chr. with small leaves and short, imbricate, ascending pinnae grow at 2800–3600 m in Ecuador and appear to be a high altitude ecotype. The smallest fertile leaves are ca. 30 cm long, in contrast to the leaves of the species which are usually 2 to 3 m or longer.

Lophosoria quadripinnata var. **contracta** (Hieron.) R. & A. Tryon, *comb. nov. Alsophila contracta* Hieron., Hedwigia **43:** 236. 1906

5. The type species of *Orthiopteris* Copel., which is a synonym of *Saccoloma* Kaulf., has not been transferred to the correct genus.

Saccoloma ferulaceum (Moore) R. &. A. Tryon, *comb. nov.* *Davallia ferulacea* Moore, Ind. Fil. 294. 1861, *nom. nov.* for *Davallia trichomanoides* Hook., 2nd Cent. Ferns t. 64. 1861, not Blume, Enum. Pl. Jav. 238. 1828.

6. *Hypolepis bivalvis* is a paleotropical species, correctly placed in the genus *Paesia,* as suggested by the epithet which refers to the two-valved indusium.

Paesia bivalvis (vAvR) R. & A. Tryon, *comb. nov. Hypolepis bivalvis* vAvR., Bull. Jard. Bot. Buitenz. II, **16:** 19. 1914.

7. Species that need to be transferred to *Ctenitis* include the following.

Ctenitis honesta (Kze.) R. & A. Tryon, *comb. nov. Polypodium honestum* Kze., Linnaea **9:** 49. 1834.

Ctenitis Tonduzii (Christ) R. & A. Tryon, *comb. nov. Aspidium Tonduzii* Christ, Pittier Prim. Fl. Costaric **3** (1): 34. 1901.

Ctenitis velata (Mett.) R. & A. Tryon, *comb. nov. Aspidium velatum* Mett., Abhandl. Senckenb. Naturforsch. Ges. Frankfurt **2:** 363 (Farngattungen IV:79). 1858.

8. *Athyrium Dombeyi* Desv., which is probably not distinct from *Athyrium Filix-femina* (L.) Roth, is the only species of the genus that occurs south of Colombia. Two species of Argentina, often placed in *Athyrium,* belong to other genera. *Athyrium decurtatum* (Link) Presl is a species of *Thelypteris,* perhaps belonging to subgenus *Amauropelta* (A. R. Smith, pers. comm.), and *Athyrium Lilloi* is a species of *Diplazium.*

Diplazium Lilloi (Hicken) R. & A. Tryon, *comb. nov. Nephrodium Lilloi* Hicken, Anal. Soc. Cient. Argent. **62:** 166. 1966. *Athyrium Lilloi* (Hicken) Alston, Lilloa **30:** 111. 1960 (received at the Gray Herbarium Library on Dec. 15, 1960); (Hicken) Morton, Amer. Fern Jour. **50:**275. 1960 (issued Dec. 23, 1960).

9. A few new combinations are needed in *Thelypteris;* and when the major groups of the genus are treated as subgenera, a name is needed for one in America.

Thelypteris subgenus **Parathelypteris** (H. Ito) R. & A. Tryon, *stat. nov. Thelypteris* section *Parathelypteris* H. Ito, Nakai & Hondo, Nov. Fl. Jap. **4:** 127. 1939.

Thelypteris brachypus (Sod.) R. & A. Tryon, *comb. nov. Nephrodium brachypus* Sodiro, Rec. Crypt. Vasc. Quit. **43.** 1883.

Thelypteris lugubris (Mett.) R. & A. Tryon, *comb. nov. Aspidium lugubre* Mett., Abhandl. Senckenb. Naturforsch. Ges. Frankfurt **2:** 378 (Farngattungen, IV: 94). 1858.

10. The large genus *Grammitis* Sw. includes about 175 American species representing six intergrading groups. Since these groups are not based on characters of major importance they are recognized as sections of *Grammitis*. One of them has traditionally been maintained as the genus *Cochlidium* Kaulf., and another is often recognized as the genus *Glyphotaenium* (J. Sm.) J. Sm.; both require a name at the rank of section. In addition, corrections are needed for two of the sectional names accepted by Morton (Contrib. U. S. Nat. Herb. 38. 1967), and several species require a name under *Grammitis*.

Grammitis section **Cryptosorus** (Fée) R. & A. Tryon, *comb. nov. Cryptosorus* Fée, Mém. Fam. Foug. **5** (Gen. Fil.): 231. 1852. *Polypodium* section *Cryptosorus* (Fée) Fourn., Ann. Sci. Nat. V, **18:** 282. 1873. *Grammitis* section *Cryptosorus* (Fee) Morton, Contrib. U. S. Nat. Herb. **38:** 90. 1967, incorrectly attributed to Fournier without basionym and invalid (Art. 33).

Grammitis section **Glyphotaenium** (J. Sm.) R. & A. Tryon, *stat. nov. Ctenopteris* subgenus Glyphotaenium J. Sm., Seemann, Bot. Voy. Herald 227. 1854 (rank assigned by C. Chr., Ind. Fil. 325. 1906) *Glyphotaenium* (J. Sm) J. Sm., Hist. Fil. 187. 1875.

Grammitis section **Grammitastrum** (Fourn.) Morton, Contrib. U. S. Nat. Herb. **38:** 89. 1967 was validly made by Morton although attributed to Fournier.

Grammitis section **Pleurogramme** (Blume) R. & A. Tryon, *comb. nov. Antrophyum* section *Pleurogramme* Blume, Fl. Jav. Fil. 69. 1828. *Cochlidium* Kaulf. Berl. Jahrb. Pharm. **21:** 36. 1820.

Grammitis achilleifolia (Kaulf.) R. & A. Tryon, *comb. nov. Polypodium achilleifolium* Kaulf., Enum. Fil. 116. 1824.

Grammitis gradata (Baker) R. & A. Tryon, *comb. nov. Polypodium gradatum* Baker, Fl. Brasil Martius, Fl. Brasil. **1**(2): 513. 1870.

Grammitis pozuzoensis (Baker) R. & A. Tryon, *comb. nov. Polypodium pozuzense* Baker, Hooker, Icon. Plant. t. 1672. 1886.
Grammitis rostrata (Hook.) R. & A. Tryon, *comb. nov. Monogramma rostrata* Hook., Sp. Fil. **5:** 122. 1863.
Grammitis venulosa (Blume) R. & A. Tryon, *comb. nov. Polypodium venulosum* Blume, Enum. Pl. Jav. 128. 1828.

11. *Loxogramme* (Bl.) Presl and *Anarthropteris* Copel. are two closely related genera, sometimes treated in a separate family. However, they share several characters with the polypodioid and grammitid ferns, which themselves are not clearly distinguished. The three groups are treated as Polypodiaceae tribe Polypodieae, tribe Grammitideae and the following.
Polypodiaceae tribe **Loxogrammeae** (Pic.-Ser.) R. & A. Tryon, *stat. nov. Loxogrammaceae* Pic.-Ser., Webbia **29:** 11. 1974.

12. Species that need to be transferred to *Microgramma* include the following.
Microgramma crispata (Fée) R. & A. Tryon, *comb. nov. Craspedaria crispata* Fée, Crypt. Vasc. Brésil 1: 119. 1869.
Microgramma geminata (Schrad.) R. & A. Tryon, *comb. nov. Polypodium geminatum* Schrad., Gott. gel. Anz. 1824: 867.
Microgramma rosmarinifolium (Kunth) R. & A. Tryon, *comb. nov. Polypodium rosmarinifolium* Kunth, Syn. Pl. Aequin. **1:** 71. 1822.

13. The following species are transferred to *Pleopeltis.*
Pleopeltis Conzattii (Weath.) R. & A. Tryon, *comb. nov. Polypodium Conzattii* Weath., Contrib. Gray Herb. **65:** 11. 1922.
Pleopeltis fuscopunctata (Hook.) R. & A. Tryon, *comb. nov. Polypodium fuscopunctatum* Hook., Sp. Fil. **5:** 69. 1863.

14. The leafy stems of *Lycopodium Trencilla* Baker (Jour. Bot. 15: 168. 1877) which may attain a length of 1 m and 3 cm in breadth, are the largest in the genus. The following comments relate to the correct spelling of the name, orthography, and author for this remarkable species. The name was first published by Baker although credited to Sodiro who is often cited as the sole author. Baker used the epithet "Transilla", probably misreading Sodiro's

handwriting, because Sodiro (Rec. Crypt. Vasc. Quit. 89. 1883) spelled it "trencilla" (a Spanish word meaning braid) and stated that this was the common name for the species. Since the epithet is derived from a colloquial name, it may properly be capitalized.

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CHROMOSOME NUMBERS OF PERUVIAN COMPOSITAE

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ABSTRACT

Chromosome numbers are presented for 36 populations of Peruvian Compositae representing 34 species distributed among 27 genera. Of these, 22 are first reports, two new generic counts (*Garcilassa*, $n = 17$ pair; *Pseudonoseris*, $n = 12$ pair). When appropriate, systematic implications of these data are discussed.

Diels (1961) was the first to make a reasonably comprehensive survey for the chromosome numbers of Peruvian species. In this he included counts for approximately 31 species of Compositae, most of these from taxa belonging to the tribe Senecioneae (*Senecio* and *Werneria*). Turner, et al. (1967) counted an additional 59 species from a broad spectrum of tribes, most of these not reported by Diels. The present contribution presents chromosome numbers for an additional 34 taxa, bringing to about 125 the list of species which have been counted from Peruvian populations.

METHODS

Counts were obtained from bud material collected in the field and pickled in 4 parts chloroform: 3 parts absolute alcohol: 1 part glacial acetic acid. Bud material was stored in a refrigerator and subsequently counted by the junior author by the well-known "squash technique" using acetocarmine stain. A complete set of voucher specimens is deposited at the Field Museum (F) and a partial set at the University of Texas (TEX).

RESULTS AND DISCUSSION

Astereae

Aster squamatus ($n = 10$), closely related to the widespread, weedy, North American species, *A. subulatus*, has been variously treated as synonymous with the latter (Nash, 1976; p. 140), or else as a distinct variety. *A. subulatus*, with the exception of one count by Turner (1978), has been found repeatedly to be diploid throughout much of its range, including collections from Mexico and as far south as Costa Rica. *Aster squamatus*, from Argentina to northern Peru, has been found to be consistently tetraploid. Shinners (1953)

treated *A. squamatus* as a variety (*australis*) of *A. subulatus*, but confused the issue by considering most of the Mexican and Central American collections as belonging to *A. subulatus* var. *australis* when, in fact, they are readily distinguished from the South American complex, not only by their diploid ($n = 5$) condition but by characters of the involucre. It would appear that the South American populations, albeit perhaps derived from populations in southernmost North America, are perhaps worthy of subspecific, if not specific rank.

Baccharis ($x = 9$)—Nearly all counts for the very large genus *Baccharis* have been diploid with $n = 9$ pairs, with the notable exception of three populations of *B. latifolia* (two from northern Peru and one from Colombia) which have been reported as tetraploid (Turner, et al., 1967; Powell & King, 1969). The present count for *B. latifolia* from central Peru (Table 1), is diploid. The closely related *B. alnifolia* is only the second tetraploid species reported for the genus, although Powell and King (1969) report an intriguing count of $n = 25$ pairs for *B. nitida*, presumably derived by aneuploid reduction at the hexaploid level.

Heliantheae

Enhydra oblonga ($n =$ ca. 50 pairs) has relatively small, numerous chromosomes that proved difficult to count. The only previous count for the genus (*E. fluctuans*) has been listed as $n = 11$ pairs (Fedorov, 1969), thus the present count would appear to be decaploid, or thereabout.

Garcilassa rivularis ($n = 17$ pairs), a monotypic genus is previously unreported. It has been positioned near *Verbesina* in the Verbesininae of Hoffmann (1894), but Stuessy (1977) realigns this with *Eclipta* and related genera in the Ecliptinae. The latter, as noted by Stuessy, mostly have base numbers ranging from $x = 11$ to $x = 16$, while *Verbesina* and cohorts are mostly on a base of $x = 17$. This suggests that *Garcilassa* is perhaps best positioned in the latter subtribe.

Spilanthes leiocarpa ($n = 16$ pairs) belongs to the typical element of the genus, as discussed by Jansen and Stuessy (1980), this being consistent with their view that *Spilanthes* (sensu stricto) is on a base of $x = 16$, while the segregate *Acmella* is on a base of $x = 12$ or 13.

Tridax peruviensis ($n = 20$ pairs) is a tetraploid on a base of $x = 10$. Powell (1965), in his study of *Tridax* ($x = 9, 10$), noted that

polyploidy was unknown in the $x = 10$ line (Sec. Imbricata). The present count establishes such ploidy and suggests, further, that the relatively few South American species were derived from their North American counterparts.

Vasquezia oppositifolia ($n = 20$ pairs) is apparently closely related to *V. anemonifolia* (HBK) Blake, which Powell and King (1969) report as $n = 19$ pairs, one population of which Olsen (1980) reported (as *V. achillioides*) to have $n = 9$ pairs. This suggests that *V. oppositifolia* is a tetraploid on a base of $x = 9$ or 10, vitiating the suggestions of Powell and King (1969) that the chromosomal base for *Vasquesia* might be "quite distinct in Bahianeae".

Liabeae

Nordenstam (1977), among others, recognizes this tribe as distinct, although Turner and Powell (1977) suggest that it might best be included as a subtribe in the Vernonieae, where its phyletic relationship appears to be (as opposed to the tribe Senecioneae where most workers have positioned the group). Regardless, the tribe has been relatively ignored until recently, when Robinson and Brettell (1973) resurrected a number of genera previously relegated to synonymy within *Liabum*. For convenience of explication the generic breakdown by these authors is followed.

Both *Chrysactinium acaule* ($n = 12$ pairs) and *C. hieracioides* ($n = 12$ pairs) have karyotypes with 11 small bivalents and 1 giant pair, as first noted by Turner, et al. (1967) for the latter species. *Liabum* itself possesses a base number of $x = 9$ (Nordenstam, 1977; Olsen, 1980). Several additional segregates from *Liabum* have now been examined (Table I): *Munnozia* ($n = 12$ pairs; previously reported as $n = 10$ pairs, Nordenstam, 1977; and $n = 9$ pairs, Olsen, 1980) and *Pseudonoseris* ($n = 12$ pairs). Thus nine of the 15 genera recognized by Nordenstam have been examined chromosomally (Nordenstam, 1977; Powell & King, 1969; present paper) with the following tally: *Chrysactinium* ($x = 12$), *Ferreyranthus* ($x =$ ca. 9), *Liabum* ($x = 9$), *Munnozia* ($x = 9, 10, 12$), *Paranephelius* ($x = 9, 14$), *Pseudonseris* ($x = 12$), *Philoglossa* ($x = 9$) and *Sinclairia* ($x = 9?$). From this assemblage it would appear that $x = 9$ is the likely base number for the Liabeae, relating the group to the Vernonieae in which base numbers of $x = 9$ and 10 predominate. This is perhaps best reflected in the morphological similarity of *Liabum* itself to the genus *Vernonia*, sections Leiboldia and Lepidonia (Turner,

Table 1. **Chromosome numbers of Peruvian Compositae**

Taxon	Voucher[1]	Chromosome no. (pairs)[2]
Tribe EUPATORIEAE		
Ascidiogyne sanchezvegae Cabr.	Cajamarca: 57 km. NE of Cajamarca. *1606.*	ca. 10
Eupatorium buddleaefolium Benth.	Cajamarca: 11 15 km. NW Celendin. *1689.*	ca. 10
Eupatorium nemorosum Klatt	Junin: 51 km NE of Tarma. *1430.*	10
Tribe ASTEREAE		
Aster squamatus (Spreng.) Hieron.	La Libertad: 4 km. NW of Coina. *1514.*	10
Baccharis alnifolia Meyen & Walp.	La Libertad: beach at Trujillo. *1531.*	18
Baccharis latifolia (R. & P.) Pers.	Junin: 19 km. NE of Tarma. *1343.*	9
Diplostephium callilepis Blake	Amazonas: 58 km. NE of Balsas. *1736.*	9
Oriotrophium hirtopilosum (Hieron.) Cuatr.	Cajamarca: 52 km NE of Cajamarca. *1590.*	18
Tribe HELIANTHEAE		
Bidens triplinervia HBK	Junin: 17 km. E of La Oroya. *1459.*	12
Coreopsis fasiculata Wedd.	La Libertad: 29 km SW of Coina. *1521.*	26
Coreopsis oblanceolata Blake	Cajamarca: 31 km. NE of Cajamarca. *1583.*	13
Coreopsis senaria Blake & Sherff	Cajamarca: 11 km. NE of Cajamarca. *1554.*	13
Coreopsis wotykowskii Sherff	Cajamarca: 23 km, SW of Celendin. *1646.*	ca. 10
Encelia canescens Lam.	Lima: ca. 150 km. N. of Lima. *1494.*	ca. 17
Enhydra oblonga DC.	La Libertad: beach at Trujillo. *1530*	ca. 50

Galinsoga quadriradiata R. & P.	Junin: 35 km. NE of Tarma. *1402.*	16
Garcilassa rivularis Poepp. & Endl.	Junin: 51 km NE of Tarma. *1422.*	17
Helianthus viridor Blake	Junin: 19 km NE of Tarma. *1329.*	ca. 17
Spilanthes leiocarpa DC.	La Libertad: beach at Trujillo. *1532.*	16
Tridax peruviensis Powell	Cajamarca: 3 km. NW of Celendin. *1680, 1680A.*	20
Tridax peruviensis Powell	La Libertad: 65 km. E of Trujillo. *1496.*	20
Tridax cf. *peruviensis* Powell	Cajamarca: 31 km. NE of Cajamarca. *1582.*	20
Vasquezia oppositifolia (Lag.) Blake	Junin: 19 km. NE of Tarma. *1327.*	20
Vasquezia oppositifolia (Lag.) Blake	Junin: 28 32 km. NE of Tarma. *1349.*	20
Verbesina sp.	La Libertad: 4 km. E of Otuzco. *1526.*	ca. 34
Tribe TAGETEAE		
Porophyllum ruderale (Jacq.) Cass.	Junin: 51 km. NE of Tarma. *1435.*	ca. 12
Tribe ANTHEMIDEAE		
Cotula australis (Sieb. & Spreng.) Hook f.	Cajamarca: 23 km SW of Celendin. *1645.*	ca. 9
Tribe SENECIONEAE		
Senecio nubigenus var. *laciniatus* (HBK) Cuatr.	Cajamarca: 13 km SW of. Celendin. *1663.*	ca. 50
Tribe LIABEAE		
Chrysactinium acaule (HBK) Wedd.	Cajamarca: 60 km. NE of Cajamarca. *1628.*	12
Chrysactinium hieracioides (HBK) Rob. & Brett.	Cajamarca: 31 km. NE of Cajamarca. *1581.*	12
Liabum floribundum Less.	Cajamarca: 33 km. SW Cajamarca. *1546.*	18

Munnozia lyrata (Gray) Rob. & Brett.	Amazonas: 30 km. SW Leimebamba. *1746.*	ca. 24
Munnozia ferreyrii Robinson	Amazonas: 43 km. NE of Balsas. *1724.*	12
Pseudonoseris szyszylowiczii Hieron.	Cajamarca: 26 km. NW of Celendin. *1699.*	12
tribe MUTISIEAE		
Onoseris albicans (D. Don) Ferreyra	La Libertad: 65 km E of Trujillo. *1495.*	18
Perezia multiflora (H. & B.) Less.	Junin: ca 140 km. E of Lima. *1481.*	8
tribe CICHORIEAE		
Hieracium lagopus D. Don	Cajamarca: 11 km. NE of Cajamarca. *1557.*	9

[1] Collection numbers are those of *Dillon & Turner.*
[2] Numbers are gametic, i.e., chromosome *pairs* observed at meiosis I.

1981). For example, *Liabum* (Sinclairia) *pringlei* Rob. & Greenm. has floral and fruit features which clearly relate the genus to the Vernonieae, the corolla, pappus, style branches, achene, and involucre being essentially like elements within *Vernonia.* Ultrastructural studies of the pollen also suggest such a disposition since members of the Vernonieae and Liabeae both possess "anthemoid" internal structural patterns in their pollen walls, as noted by Skvarla et al. (1977) and Bolick (1978).

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A NEW SPECIES OF TITHONIA (COMPOSITAE) AND INFRAGENERIC CLASSIFICATION

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A revision of *Tithonia* (LaDuke, 1980) necessitates some nomenclatural additions and the description of a new species.

Tithonia hondurensis LaDuke, *sp. nov.*

TYPUS: HONDURAS, El Paraiso, 5 mi W of dirt rd. to Ojo de Agua and highway from Danli to Zamorano (Hwy. 4), 4 Dec 1978, *V.A. Funk, K. Landon 2938* (HOLOTYPUS, OS!; ISOTYPUS, F! NY!).

Frutex, erectus, perennis, 0.5–4 m altus. Caules rotundati, fusci, moderate hispidi vel glabri. Folia alterna, sessilia aut petiolata, petiolis 4 mm longis; laminae lineares-lanceolatae, interdum basi duobus lobis parvis, (3) 6.5 23 cm longae, (0.5–) 1.5–2.8 cm latae, apice acuminatae, basi attenuatae vel rotundatae-attenuatae, supra pubescentes pubibus densis brevibus, subter longioribus tomentosae, margine integrae vel serratae crenataeve, revolutae. Pedunculi 8.5–25 cm longi, 3 7 mm diametro, sparsim vel moderate hispidi prope capitula, infra deminuti. Capitula plerumque solitaria. Receptacula (5–) 10–15 mm diametro. Phyllaria 20–30, in quatuor seriebus, linearia vel spathulata, apice rotundata; bracteae extimae 4.5–8 mm longae, 2–4 mm latae, abaxialiter modice puberulae; bracteae intimae 7–11 mm longae, 2–4 mm latae, apice rotundatae, abaxialiter glabrae. Paleae striatae, 6.5–9 mm longae, 0.75–2 mm latae; apex acutatus, 0.5–1 mm longus, interdum lateraliter lobatus, minute pubescens. Flosculi radii 13–15; ligulae luteae, lineares vel ovatae, (13–) 18–42 mm longae, 6 10 mm latae, apex trifidae; tubi 1 1.5 mm longi, 0.5–0.75 mm diametro; pappus nullus; achenia in una serie, triangularia, alba. Flosculi disci 60–80; corollae luteae, lobis 5, 0.75–1 mm longis, 0.5 mm latis, apice acutis; faux cylindrica cum basi expansa minute puberula, parte cylindrica 2.5 3 mm longa, 0.75 1 mm diametro, parte expansa 1–2 mm longa, 1 mm diametro; tubus minute puberulus, 0.5 1 mm longus, 0.5 0.75 mm diametro; antherae nigae, 3–4 mm longae; stylus 5.75 7 mm longus; stigmata papillata 1.5–1.75 mm longa; pappus nullus; achenia nigra, rotundata quadrangularia, 3.5 mm longa, 1.5 mm diametro, basi eliasomate. Chromosomatum numerus, $n = 17$.

PRINCIPAL FLOWERING TIME: November–March

DISTRIBUTION: Belize and Honduras

REPRESENTATIVE SPECIMENS: BELIZE. **Cayo:** 15 Mar 1960, *Hunt 295* (LL, BM); Makal River at end of Kinloch rd, 22 Jan 1970, *Spellman 1412* (MO). HONDURAS. **Comayagua:** 3 km S of Siguatepeque, 9 Jan 1969, *Molina 23298* (F, MO, NY, US); ca 20 mi SE Comayagua on rte 1, 29 Oct. 1976, *Stuessy & Gardner 4420* (OS). EL PARAISO: Manzaragua rd, 5 Jan 1947, *Williams 11497* (F, GH, MEXU); 8 km N of Yuscaran, 30 Nov 1952, *Williams & Williams 18655* (F, GH, LL, US); NE of Danli, 15 Mar 1957, *Molina 7599* (F); in Pine Forest of Guayabillas Road to Ojo de Agua, 23 Nov 1970, *Molina 25904* (DUKE, F, MO, NY, U).

Tithonia hondurensis is a small shrub and is most closely related and similar to *Tithonia longiradiata* (Bertol.) S.F. Blake. It can be most easily distinguished from it by its smaller stature, smaller heads, and revolute leaf margins. Larger plants are distributed in Belize and diminutive plants are found in the area of Sigatepeque, Honduras. *T. hondurensis* has the same number of chromosomes as all the *Tithonia* taxa, with $2n = 34$. Illustrations, distribution map and additional comments may be found in La Duke (1980, and in press b).

GENERIC SUBDIVISION

The following infrageneric divisions are validated prior to a publication concerning the flavonoids of the genus (La Duke, 1982a).

Tithonia Section *Tithonia*

Series **Tithonia**

Herbaceous annuals; leaves deltate to 3–5 lobed; involucre 2–3 seriate. TYPE SPECIES: *Tithonia rotundifolia* (Mill.) S. F. Blake.

Series **Grandiflorae** La Duke, *ser. nov.*

Plantae perennes fruticosae aut arborescentes; folia petiolata, laminis deltatis vel lobatis; ligulae plus quam 45 mm longae.

TYPUS: *Tithonia koelzii* McVaugh.

Series **Fruticosae** La Duke, *ser. nov.*

Plantae perennes suffruticosae; folia lanceolata, sessilia aut petiolata; phyllaria in tribus aut quatuor seriebus; achenia quadrangu-

laria. TYPUS: *Tithonia fruticosa* S. M. Canby & J. N. Rose in J. N. Rose.

Tithonia Section **Mirasolia** (Sch.-Bip. in Seemann) La Duke, *stat. nov. Tithonia* Gmelin Subgen. *Mirasolia* Sch. Bip. in Seemann

Perennial shrubs; leaves linear to ovate, usually sessile to short-petiolate, margins serrate to crenate; phyllaries 3–4 (–5)-seriate; disk achenes rounded-quadrangular, epappose, glabrous, with eliasome at base. TYPE SPECIES: *Tithonia calva* Sch.-Bip. in Seemann.

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OLOF SWARTZ IN BOSTON, 1783

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On his way to the West Indies Olof Swartz stayed eight weeks in Boston. He gave an account of his visit in a letter home, published in *Upfostrings—Sälskapets Tidningar*. A reference to this obscure publication had been given by Wikström (1829: xxxiv) in his biography of Swartz. Nevertheless, Hooker (1840: 383) in an appreciation of the famous Swedish botanist wrote that he "passed a year in North America". Subsequently Sargent (1947: 44) in a footnote in the Silva of North America repeated the fact stating "Having spent a year in North America, he visited the West Indies".

The references to Swartz being in North America for a year are false, however, and the story of his visit to Boston has remained largely unknown, although Rydberg (1907: 16) gave the correct dates of his arrival and departure, stating that Swartz "sailed in a merchant vessel to Boston, where he landed the 3rd of October. He did not intend to stay there, but took the first opportunity offered him to go to Jamaica. He left Boston on the 26th of November . . ." Stearn (1980: 2) recently wrote of Swartz's contributions to West Indian Botany, and noted, "On 5th August 1783, having completed his studies in medicine and natural history at the University of Uppsala, where he had been a student of the younger Linnaeus, Swartz sailed from his native Sweden for North America. He was twenty-two years old and furnished with adequate private means . . . It took Swartz five months to get there (Jamaica), two months longer than Sloane had taken in 1687, for he voyaged first to Boston, Mass., observing "Pingvine" (Great Auk, *Alca impennis*) off the Newfoundland banks, where these now extinct flightless birds were slaughtered so prodigally and mercilessly. He arrived on 3 October 1783. A letter, printed in *Upfostrings-Sälskapets Tidningar* (Stockholm) 1784 no. **27** (8 April 1784), describes his Bostonian botanizing. He left Boston on 26 November 1783 aboard a ship bound for Jamaica . . ."

During his stay in Boston Swartz also collected specimens and they are now in the general herbarium in Stockholm (s). Unfortunately, Swartz hardly made any annotations on his specimens. He only wrote the name of the plant on the back of the sheets and 19th century curators (Wikström) have marked the sheets "Herb. Swartz"

and in a few cases only "ex Amer. Sept." In a letter to P. J. Bergius, printed in *Läkaren och Naturforskaren* **8:** 327 334 (1787), Swartz mentioned that he also sent a few packets of North American herbs to Bergius. Apparently these were lost, however. Swartz stated that he "then never heard of them but there is all reason to believe that they were lost in the autumn gales". There are no Swartz specimens from North America in Bergius' herbarium (SBT).

To the following translation of Swartz's letter we have added in parentheses the modern equivalents of the species listed as well as an s if there is a Swartz specimen in Stockholm. It should be noted, however, that these specimens may have been collected elsewhere, since Swartz failed to give any localities on his specimens. In a few cases it is not clear what plant Swartz had in mind and this is indicated by a question mark.

"Oct. 2, 1783. A tongue of land called Cape Anne became our first touch of land at the destination of the journey. We all beamed with joy. Several kinds of land birds: falcons and sparrows flew around the ship. *Certhia pusilla* (brown headed nuthatch) then became a nice present for me. Towards the evening the whole extension of this land met us and at 3 o'clock p.m. we were already among the rocks, where the meeting with the guides became as agreeable as that with the land birds. We now had no more than 12 English miles left, and this way, which was between the most beautiful of sights, was covered before the evening, when we had the whole of Boston in view. We anchored here at the Kings-Road and came the day after closer to the city. The view from this harbour is similar to that of an amphitheatre, where hundreds of ships cover the bridges towards the sea-side. We considered our early arrival so much more fortunate, since a Danish ship, which had spent 4 whole months on the sea, recently had arrived.

Oct. 3. After 30 days spent on the sea, I now had the joy of putting my feet on solid ground, on a land where nothing but Freedom reigns; a place, which still can be compared to the society of an ant-hill. Boston is a town, which not all geographers have neglected to describe, but I must mention that the town is 4 English miles, and it has 16 churches. Outside the houses there are the American elm, linden, the white walnut tree etc. Gardens are here of considerable value. Every house has its own, and much money is spent on it. In these there is an abundance of *Cucumeres* & *Cucurbitae,* which surround both windows and doors. *Chrysanthema, Verbasca. Aco-*

nita, Delphinia and several European herbs decorate these gardens. The flora now had lost its prosperous summer appearance so there was not much for me to get. However, I visited on the 6th, 9th and 12th of this month the shores of the bay. *Panicum crus-corvi* (*Panicum crus-galli,* s), *Amaranthus hypochondriacus* (s), *Amaranthus lividus, Acalypha virginica* (s), *Potentilla canadensis* (s), *Potentilla norvegica, Viola primulaefolia* (s), *Portulaca oleracea, Euphorbia maculata, Salicornia virginica* (s), *Phytolacca decandra, Dactylus cynosuroides* (?), *Erigeron canadensis* (s), *Sarotra* (*Hypericum*) and the following, *Salsola rosacea* (NB calycibus explanatis corolliformibus & corollatis) (*Salsola kali,* s), *Salsola salsa* (*Suaeda maritima,* s), *Aster linifolius* (*Aster subulatus*), *Aster novae-angliae, Mollugo verticillata* (s), *Ambrosia elatior* (*Ambrosia artemisiifolia* var. *elatior,* s) and others were still to be found as well as our *Carduus lanceolatus* (*Cirsium vulgare*) and *Polygonum aviculare,* which seem to follow Man all over the Earth. The late gathering of this Flora was a great joy to me. Of my highly beloved cryptograms I have seen no others than those which are common to the whole North. The insects have not left me without any shares, which is proven by a big and beautiful *Papilio, Gryllus carolinus, Gryllus danicus* (both crickets), *Gryllotalpa* etc.

I intend to visit the towns in the neighborhood and among those New Cambridge, remarkable because of its academy, which however is still said to be in its beginning. On the 6th this month a professor of medicine was installed there [Professor Benjamin Waterhouse]. But no foreigner has yet been accepted as a teacher.

Oct. 8. I went out somewhat more than a Swedish mile (6 English miles) from the town, to see what was left of the Flora. *Uniola maritima* (?), *Aster tardiflorus, Conium rigens* (*Conium maculatum*?), *Bidens frondosa, Coreopsis bidentis* (*Bidens cernua*?), *Polygonum maritimum* (*Polygonum glaucum*), *Datisca cannabina* (s), *Cannabis sativa* (s), *Chenopodium maritimum* (*Suaeda maritima,* s), *Salicornia vulgaris, Salsola rosacea* (*Salsola kali,* s), *Tanacetum vulgare, Sonchus* and *Dactylis* were all that I found.

Oct. 15. The cold was now so strong that despite a constant fire in my rooms, the thermometer never rose above 10 degrees.

Oct. 18. During an excursion, which today was held about a Swedish mile from the town, I again came across *Sarotra gentianoides* (*Hypericum gentianoides,* s), *Vaccinium ligustrinum* (*Lyonia ligustrina,* s), *Hyoseris virginica* (*Krigia virginica,* s), *An-*

tirrhinum canadense (*Linaria canadensis,* s), *Juniperus virginiana* (s), *Cupressus thyoides* (*Thuja occidentalis*), *Stipa capillata, Solidago canadensis, Scirpus tristachius* (?), *Aster linarifolius,* three or four new species of lichens and one *Polygonum,* which however like Kalm's (*Polygonum*) *erectum* must be something new.

Mr Richard Söderström, who not only in New York but also here in Boston is Royal Swedish Consul, has everywhere gained such confidence, and I am pleased with the many and great acquaintances to whom he has introduced me. The way of life here is beyond all my praise, since it seems that the newly acquired freedom has led to a laudable as well as a great courtesy towards strangers. At least I enjoy a greater respect and courtesy than I could and should have expected in such a distant country. Seemingly good financial resources must be the reason why I have had to pay 8 piasters (dollars) a week for board and lodging. This will soon put an end to my travelling funds. Consequently I have tried to become a ship's doctor but I received the answer that those are not hired during peace time. Nevertheless I continue the journey with the small amount of money I still have: Audaces Fortuna juvat! However, if I could get some kind of subsidy, some public grant, I could stay here so much longer and get so much more done for the benefit of science, for the development of which I am here. Ternström, Kalm, Hasselqvist, Torén, Osbeck, Löfling, Köhler, Rolander and Martin had their salaries; but like Montin, Bergius, Solander, Baron Alströmer, Falk, Thunberg and Sparrman I had to travel on my own accounts without any public grants.

I must not forget the women! Of them I can say no more than that Nature here has provided them with all kinds of attractions. They are also in this province considered to take precedence over those from other colonies. All entertainment, comedy, tragedy, opera is here forbidden. However, some ball is now and then arranged, but this is very seldom. Next week I will travel 60 or 70 English miles further down the country and in the company of Mr. Consul Söderström, and my friends will be informed about everything that I manage to observe during the journey.

Olof Swartz"

The "Kings-Road" anchorage Swartz mentioned is now called President Road or Broad Sound and is the entrance to the inner harbor of Boston between Deer Island and Long Island. Landing on Deer Island one can walk to Winthrop, Revere and the North Shore. Most of the plants Swartz named can be found in the area today. However, several botanical names can not be placed, and specimens which reveal their correct identity have not been located. The binomials *Conium rigens, Coreopsis bidentis,* and *Scirpus tristachius* can not be associated with any modern species. *Dactylis cynosuroides* may be *Spartina cynosuroides,* which is represented in the herbarium of the New England Botanical Club by single specimens from the New Hampshire-Massachusetts border and from Plymouth, Massachusetts. *Uniola maritima* is suggestive of *Uniola paniculata,* a species not found north of Virginia. *Cannabis sativa* may have been valued at that time as a source of fiber or seed. It certainly does occur in the Boston area today but is poorly represented by modern collections in herbaria. *Datisca cannabina* does not appear to be recorded from the United States. The Swartz specimen (s) does not bear a geographic location, but Swartz would have known this European plant.

In Swartz's other letters there is no reference to his intended trip of 60–70 miles farther into the country or to his activities during the end of October and November before his departure for Jamaica. There is also no record whether Swartz sent his Boston collections directly to Sweden or carried them with him to Jamaica.

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BRYOPHYTES OF THE FLUME, FRANCONIA NOTCH STATE PARK, N.H.

JANICE M. GLIME

The Flume at Franconia Notch State Park is a welcome retreat for visitors who seek relief from the heat of the summer. Its steep walls and constant splash of mountain water plummeting over the waterfall at its summit provide a form of natural air conditioning sufficient to convince anyone that the heat of summer is far away. On these walls, one would expect bryophytes which are adapted to a cool, northern climate.

In 1908 the Sullivant Moss Society collected liverworts throughout the Franconia Mountains and reported on the liverworts of the Flume (Lorenz, 1908). There is no report of Flume mosses.

Our objectives were to establish a checklist for the mosses, to compare the liverworts to the 1908 study, and to determine if the cool, moist atmosphere of the Flume truly was inhabited by bryophytes with a northern distribution.

The Flume is about 210 m long, 3–5 m wide, and 18 m deep (Lorenz, 1908). The walls are of coarse granite and their faces, ledges, and crevices are constantly wet from the splash of the Flume Brook cascade. These walls are well-covered with a variety of bryophytes, and vegetation on ledges and in cracks is quite lush.

Three of us sampled extensively for two days to be certain that we had a representative of each species.

The Flume is a very good place to study northern bryophytes adapted to wet or moist rocks. Its flora is well developed and the species occurring there are predictable. All of the species we found are typical of the northern Coniferous Forest Zone (Howard, 1975; Schuster, 1953; Steere, 1978), though their ranges frequently extend farther north and south.

Several microhabitats can be identified, and the bryophytes which occupy them differ. We identified 34 species of mosses and 14 species of liverworts within the Flume. Table 1 separates these by vertical walls, cracks and crevices, and horizontal or sloping ledges.

All the liverworts but *Bazzania denudata* had been found in the Franconia Mountains by The Sullivant Moss Society in 1908 (Lorenz, 1908). Since most were common species, Lorenz did not cite the Flume specifically. Our only certain additions to the 1908

Table 1. **Presence of bryophytes on vertical walls, cracks and crevices, and ledges and bases within the Flume, Franconia Notch State Park, N.H.**

	Wall	*Crack*	*Ledge*
Andreaea rupestris Hedw.		———	
Fissidens osmundioides Hedw.		———	
Grimmia alpicola Hedw. var. *rivularis* (Brid.)Wahl.		———	
Grimmia apocarpa Hedw. var. *conferta* (Funck)Spreng.		———	
Isopterygiopsis muelleriana (Schimp.)Iwats.		———	
Isopterygium elegans (Brid.)Lindb.		———	
Mnium marginatum (With.)Brid. ex P.-Beauv.		———	
Plagiothecium denticulatum (Hedw.)B.S.G.		———	
Sematophyllum demissum (Wils.) Mitt.		———	
Anastrophyllum minutum (Cr.)Schuster		———	
Bazzania denudata (Torrey ex Gott. et al.)Trev.		———	
Bazzania tricrenata (Wahlenb.)Lindb.		———	
Blepharostoma trichophyllum (L.)Dumort.		———	
Marsupella emarginata (Ehr.)Dumort.		———	
Mylia anomala (Hook.)Gray		———	
Plagiochila aspleniodes (L.)Dumort.		———	
Ptilidium pulcherrimum (Web.)Hampe		———	
Tritomaria exsecta(Schmid.)Schiffn.		———	
Bartramia pomiformis Hedw.		———	
Dicranella heteromalla (Hedw.)Schimp.		———	
Pohlia cruda (Hedw.)Lindb.		———	
Brachythecium plumosum (Hedw.)B.S.G.	———		———
Herzogiella striatella (Brid.)Iwats.	———		———
Hypnum imponens Hedw.	———		———
Scapania nemorosa (L.)Dumort.	———		———
Paraleucobryum longifolium (Hedw.)Loeske.	———		
Philonotis fontana (Hedw.)Brid.	———		
Amphidium mougeotii (B.S.G.)Schimp.		———	
Isopterygium distichaceum (Mitt.)Jaeg. & Sauerb.		———	
Mnium punctatum Hedw. var. *elatum* Schimp.		———	
Lepidozia reptans (L.)Dumort.		———	
Pogonatum alpinum (Hedw.)Rohl.		———	
Rhabdoweisia crispata (With.)Lindb.		———	
Atrichum undulatum (Hedw.)P.-Beauv.			———
Brotherella recurvans (Mx.)Fl.			———
Campylium chrysophyllum (Brid.)J. Lange			———
Dicranum scoparium Hedw.			———
Drepanocladus uncinatus (Hedw.)Warnst.			———
Hylocomium splendens (Hedw.)B.S.G.			———
Hygrohypnum luridum (Hedw.)Jenn.			———
Rhacomitrium aciculare (Hedw.)Brid.			———
Rhacomitrium heterostichum (Hedw.)Brid.			———
Sphagnum recurvum P.-Beauv. var. *tenue* Klinggr.			———

Sphagnum squarrosum Crowe ———
Thuidium delicatulum (Hedw.)B.S.G. ———
Bazzania trilobata (L.)S. Gray ———
Conocephalum conicum (L.)Dumort. ———
Pellia Raddi ———

Flume liverwort list are *Bazzania denudata* and *Mylia anomala.* Of greater interest is the list of liverworts we could no longer locate on the Flume walls: *Preissia quadrata* (Scop.) Nees; *Lejeunea cavifolia* (Ehrh.) Lindb. emend. Buch; *Aneura pinguis* (L.) Dum.; *Plectocolea hyalina* (Lyell) Mitt.; *Jungermannia pumila* With.; *Gymnocolea inflata* (Huds.) Dum.; *Tritomaria quinquedentata* (Huds.) Buch; *Scapania curta* (Mart.) Dum.; and *Scapania apiculata* Spruce.

Of the 17 bryophytes restricted to the vertical walls, 9 were liverworts. These were all leafy and mostly very small species. *Plagiochila asplenioides* stood out as shelves and was therefore the most conspicuous liverwort.

The mosses restricted to the vertical walls were either small cushion or tuft-forming acrocarpous species (5) or small mat-forming pleurocarpous ones (3). The relatively rare *Isopterygiopsis muelleriana* occurred here in long dripping strands. *Herzogiella striatella* was the most common moss, and *Andreaea rupestris* was also abundant. Larger acrocarpous species were invading near crevices or ledges, but these were often atypical, depauperate forms (*Bartramia pomiformis, Paraleucobryum longifolium, Philonotis fontana*).

The crevices had only four species restricted to them, but shared eight species with either vertical walls or ledges. *Amphidium mougeotii* was the most abundant of the restricted species. *Amphidium mougeotii* was the most abundant of the restricted species. *Isopterygium distichaceum* was found only on the ceiling of rock crevices. *Rhabdoweisia crispata* was the dominant crack and ledge species, although *Philonotis fontana* was dominant in the wettest places. *Pogonatum alpinum* formed large clumps where soil accumulated.

The strictly ledge species were all larger species and many of them could be found in the forest as well. *Campylium chrysophyllum* was found only on the floor of a small cave above the falls. *Hygrohypnum luridum* is a rare species and occurred only on the dripping, sloping rock faces. The only two thallose liverworts of the Flume,

Conocephalum conicum and *Pellia* sp., occurred at the base of the Flume wall.

The Flume Brook had *Rhacomitrium aciculare* on emergent rocks and *Scapania nemorosa* on bedrock near the edge. *Philonotis fontana* was abundant on wet rocks.

The species present, as expected, have northern distributions and high moisture requirements. Their abundance on the Flume walls provides a good lesson in bare rock succession.

ACKNOWLEDGMENTS

I appreciate the help of Frank Bowers, Barbara Hoisington, Norton Miller, William Steere, William Zales, and Richard Zander in checking my determinations. Field work was assisted by Riley Burdett and Roana Holcomb.

Voucher specimens are in the Michigan Technological University Cryptogamic Herbarium (MTUCH).

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ANOTHER ALIEN IN THE CALIFORNIA FLORA[1]

REED C. ROLLINS

It has taken a second "encounter" in which an inordinate amount of time was spent tracking down a crucifer that appeared to be native to the California flora to convince me that all alien plants growing without cultivation should be recorded and made known in some way. Had I done so in 1954 when an *Aubrietia* was first determined to genus and tentatively identified as to species from specimens collected on Hull Mountain near the border of Lake and Mendocino counties, California, by Rimo Bacigalupi and G. Thomas Robbins, it would have saved both me and Thomas W. Nelson of Humboldt State University a lot of time and effort. The first time around, material in fruit was sent from Berkeley as a *Draba* to C. L. Hitchcock for identification but since the plants were not of that genus, specimens eventually came to me. Clearly the plants were of no known genus of the Cruciferae native to California, although there were certain features resembling *Draba* and others reminding me of *Arabis parishii* of southern California. However, flowering specimens were essential to work out a positive identification even to genus. Bacigalupi and Robbins went back to the summit of Hull Mountain on June 7, 1955, and collected good flowering specimens. With these in hand, it was possible to say *Aubrietia* with certainty and give the probable full identity as *Aubrietia deltoidea* (L.) DC. (?), and it was left at that.

The next episode for me began in early 1980 when specimens in fruit of an unknown crucifer tentatively placed in *Lesquerella* were sent for identification. These were collected at the top of Hull Mountain on July 14, 1977 by J. P. Smith, J. O. Sawyer, and T. W. Nelson. Having forgotten about the earlier encounter with *Aubrietia* posing as a native, and knowing full well the specimens were not *Lesquerella,* I asked for flowering material thinking something new in the native flora had been discovered. A trip to the site for flowering specimens was made by Tom Nelson, and again with the specimens he obtained available for comparison, their identity as *Aubrietia* was made with certainty.

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[1]Results presented in this paper were obtained through support by grant GEB 78-08766 from the National Science Foundation.

How did *Aubrietia* get to the top of Hull Mountain at an elevation of about 6,800 ft? There is a forest fire look-out station there. Possibly someone deliberately scattered seeds at the site. In any case, the plants are growing without cultivation in crevices of "tight-fitting" scree and around rocks, habitats not unlike those where several species of *Aubrietia* grow natively in the eastern Mediterranean region of Europe.

Aubrietia deltoidea is the source of a number of cultivars and is grown in rock gardens and borders. It is naturalized in western Europe and elsewhere and it would be a good candidate to become naturalized in North America. However, the Hull Mountain specimens do not fully accord with native material of *A. deltoidea* in at least two respects. The siliques are densely and uniformly covered with minute dendritic trichomes in the Hull Mountain material whereas in *A. deltoidea* there is a mixture of large, mostly bulbous based, simple or forked trichomes and minute dentritic ones. This feature is used in keys to separate *A. deltoidea* from other species. A second difference is in the leaves. In *A. deltoidea,* the leaves are obovate or deltoid in outline and are dentate with two to several broad teeth. The Hull Mountain material has mostly entire, oblong to oblanceolate leaves. The cultivars of *A. deltoidea* show that the species is quite variable and a number of relatively divergent types have been developed for cultivation. If, as I suspect, the Hull Mountain population arose from a cultivar source, the differences from wild specimens of *A. deltoidea* are explainable. For the present, it seems best to refer the California specimens to *A. deltoidea* (L.) DC. without attempting to find out to which variety or cultivar they are most comparable. At the same time, the possibility that some other species of *Aubrietia* may be represented should be kept in mind.

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NEW ENGLAND NOTES

NEW STATIONS FOR *CAREX LIVIDA* VAR. *GRAYANA* AND *DRYOPTERIS FRAGRANS* IN WASHINGTON COUNTY, VERMONT

PETER F. ZIKA

The only documented station for *Carex livida* (Wahlenberg) Willdenow var. *grayana* (Dewey) Fernald in Vermont has been from Bristol Pond Bog in Bristol, Addison County. The station was discovered in 1879 by Cyrus Pringle. The last collection in Bristol was by Eggleston and Dike in 1898 (Seymour, 1969). Countryman (1978) included the species in his list of Vermont's rare and endangered plants.

My June visit to a fen near Chickering Road in Calais yielded the second known station for *Carex livida* var. *grayana* in Vermont. A vigorous colony was growing in shallow water with *Carex stricta* Lamarck, *Cladium mariscoides* (Muhlenberg) Torrey, *Scirpus hudsonianus* (Michaux) Fernald, *Eriophorum viride-carinatum* (Engelmann) Fernald, and other sedges too immature to identify so early in the season. Specimens (*Zika # 1481*) are on deposit at the herbarium of the University of Massachusetts (MASS) and at the Pringle Herbarium (VT).

Another species which Countryman (1978) listed as endangered in Vermont is *Dryopteris fragrans* (L.) Schott, a rare and local plant in northern New England. An alpine station for *Dryopteris fragrans* has been known from the cliffs forming the southern face of Camels Hump summit since Pringle's 1876 visit to the mountain. That colony persists on the south-facing summit ledges at 3800 feet, growing with *Woodsia glabella* R. Brown as it does in Smugglers Notch.

At 3000 feet a cliff rises between the Green Mountain Club's Forestry Trail and Alpine Trail, approximately one-half mile to the east of the summit of Camels Hump, in Duxbury. On the north end of these schist ledges is a previously unrecorded station for *Dryopteris fragrans*. The colony consists of nearly 25 plants, and is easily located by first finding the colorful orange lichens nearby (tentatively identified as *Xanthoria elegans* (Link) Th. Fr.). In lieu

of a specimen a photograph has been deposited at the Pringle Herbarium (*Zika 77-3-13*).

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A NEW RECORD OF SCARLET OAK IN SOUTHWESTERN NEW HAMPSHIRE

WAYNE E. MANNING

Scarlet Oak (*Quercus coccinea* Muench.) has not previously been recorded from Cheshire County, New Hampshire. It is listed in Frank Seymour's *Flora of New England* from only Rockingham and Hillsborough Counties in New Hampshire, and is not listed in David E. Boufford's recent mimeographed "Checklist of plants of Cheshire County, New Hampshire" (Department of Biology, Keene State College, Keene, NH).

One specimen grew vigorously in very sandy soil at Forest Lake, Winchester (southwestern Cheshire County), but was cut in August 1980. The tree produced many immature acorns, but only a few mature ones, as there were no other Scarlet Oaks in the area to provide pollen. The stump was 57 inches in circumference and showed at least 60 growth rings; the tree is thought to have been about 80 years old. After the cutting and clearing away, a few twigs with brown leaves and rather poor buds were salvaged. These specimens are in the herbaria of Keene State College, NEBC, and BUPL.

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THE 1981 JESSE M. GREENMAN AWARD

The 1981 Jesse M. Greenman Award has been won by William R. Buck for his publication "A generic revision of the Entodontaceae" (J. Hattori Bot. Lab. **48:** 71 159. Aug. 1980). This monographic study is based on a Ph.D. dissertation from the Department of Botany, University of Michigan, Ann Arbor.

The Greenman Award, a cash prize of $250, is presented each year by the Alumni Association of the Missouri Botanical Garden. It recognizes the paper judged best in vascular plant or bryophyte systematics based on a doctoral dissertation which was published during the *previous* year. Papers published during *1981* are now being considered for the 15th annual award, which will be presented in the summer of 1982. Reprints of such papers should be sent to: Greenman Award Committee, Department of Botany, Missouri Botanical Garden, P.O. Box 299, St. Louis, MO 63166, U.S.A. In order to be considered for the 1982 award, reprints must be received by 1 July 1982.

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The Northeastern Section of

THE BOTANICAL SOCIETY OF AMERICA

will hold its 1982 Field Meeting June 14–15–16 at Framingham, Massachusetts, with the New England Wild Flower Society as host organization. For details contact:

Mary M. Walker, Chairman
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RHODORA January 1982 Vol. 84, No. 837

CONTENTS

A monograph of the genus Malvastrum A. Gray (Malvaceae:Malveae)
Steven R. Hill 1

Experimental taxonomy in the genus Amelanchier II: Do the taxa in the genus Amelanchier form an agamic complex?
W. Ann Robinson 85

Checklist of the Alpine flora of Western Brook Pond and Deer Pond areas, Gros Morne National Park
Alexander Robertson and *B. A. Roberts* 101

Nesting of beetles and ants in Clibadium microcephalum S. F. Blake (Compositae:Heliantheae)
Guy L. Nesom and *Tod F. Stuessy* 117

Additional taxonomic and nomenclatural notes on ferns
Rolla Tryon and *Alice F. Tryon* 125

Chromosome numbers of Peruvian Compositae
Michael Dillon and *B. L. Turner* 131

A new species of Tithonia (Compositae) and infrageneric classification
John C. LaDuke 139

Olof Swartz in Boston
Richard A. Howard and *Kåre Bremer* 143

Bryophytes of the Flume, Franconia Notch State Park, N.H.
Janice M. Glime 149

Another alien in the California flora
Reed C. Rollins 153

NEW ENGLAND NOTES:

New stations for Carex livida var. grayana and Dryopteris fragrans in Washington County, Vermont
Peter F. Zika 155

A new record of Scarlet Oak in southwestern New Hampshire
Wayne E. Manning 156

Announcement of the 1981 Jesse M. Greenman Award 157

Announcement of the 1982 Field Meeting of the Botanical Society of America . . . . . Inside back cover

Rhodora

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Cover illustration

Sagittaria cuneata, a northern species, is fairly common in northern New England, rarer to the South except down the Rockies. The species is variable, often producing flat, linear leaves similar to *Vallisneria americana* when growing submerged in rivers.

Original art by Pamela Bruns, reprinted here by permission from Hellquist, C. B., & Garrett E. Crow, *Aquatic Vascular Plants of New England. Part 3. Alismataceae*, New Hampshire Agr. Expt. Sta., UNH, Durham, N.H.

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A MONOGRAPH OF MALVASTRUM, II[1]

STEVEN R. HILL

TAXONOMIC TREATMENT

The species of *Malvastrum* are distinguished by means of unique combinations of diagnostic morphic and karyological characters that vary within prescribed limits. Each species is thought to consist of potentially or actually interbreeding populations with a definable common ancestor, the majority of whose characters are retained by each population. The species presented in this treatment are not known to intergrade (no indisputable natural hybrids have been seen) and so seem to be reproductively isolated. This isolation is most evident from the fact that some species occur in the same geographic area without hybridization. Changes in chromosome number, particularly differences in ploidal level, have been a major cause of speciation through reproductive isolation.

The subspecies within a given species of *Malvastrum* have been distinguished from species by their lack of potential crossing-barriers, by a conformity in the majority of their morphological characters, and by their geographic integrity. In areas of contact between subspecies, a very few intermediate individuals may occur. In the greenhouse, the subspecies that were grown were successfully crossed and produced viable seed. Each subspecies possesses a unique set of diagnostic characters, fewer in number than those distinguishing species, that reflects a period of geographic isolation and ecological adaptation in its history. Characters such as

[1]This is the second of three parts. Part I, containing the introduction and the general discussion of the genus, was published in Vol. 84, No. 837 (Jan., 1982). Part III, concluding the Taxonomic Treatment and including the Literature Cited and the Appendices, will appear in Vol. 84, No. 839 (July, 1982).

flowering and fruiting behavior, as well as morphic characters are generally very important at the subspecies level in the genus.

Varieties have been distinguished in two cases in which the morphological variant is sympatric with the typical variety. Naming these as new varieties will facilitate information retrieval for these significantly different individuals. They are defined by one or more easily distinguishable characters that are not found in the typical members of the population. Since the sympatric nature of the individuals obscures their evolutionary history, they have been relegated to the position of morphological variants within an interbreeding population rather than subspecies. The varietal category is useful in analyses of total population variation and allows one to refer to distinctive individuals within that population.

The taxa in this treatment have been arranged in approximately the same order presented in Fig. 18 and are numbered in the key and text in accordance with the OTU code presented in Appendix II. Morphological terms have, for the most part, followed the definitions in Radford et al. (1974). Measurements listed are based upon the total variation observed in both living and preserved specimens. The extremes are included within parentheses.

GENERIC DESCRIPTION

Malvastrum A. Gray, Mem. Amer. Acad. Arts n.s. **4**: 2, in adn. 1849.

TYPE: *Malvastrum wrightii* A. Gray [= *M. aurantiacum* (Scheele) Walpers]. *Sidopsis* Rydberg, Fl. Prairie Plains Centr. N. Amer. 541. 1932.

Suffrutescent or herbaceous perennials or annuals (0.2) 0.5 2 (3) m tall with one to several ascending or erect fibrous to soft-woody *primary stems* 1 15 mm in diam at base, monopodially branched but usually sparingly so, branch apices green and herbaceous; *vesture* of vegetative parts with closely appressed or tufted, occasionally tuberculate or pustular-based, (2) 4 12-rayed stellate hairs, or, less frequently, sub-lepidote or simple hairs 0.05 2 mm diam; *cotyledons* ovate, subcordate truncate to wide-cuneate at the base and retuse to rounded at the apex, entire or rarely the blade obscurely 3-lobed, (6) 7 18 mm long × (7) 8 13 mm wide, petioles 3–9 mm long; *stipules* appressed or reflexed, wide-lanceolate, narrowly triangular to linear, usually falcate, long-acuminate to

subulate, (2) 3–9 (16) mm long × 0.2 1.5 mm wide, drying early and caducous or persistent, appressed-pubescent or strigose at least on the abaxial surface, the margin entire to irregularly toothed and often ciliate, with 1 5 parallel veins; *petioles* (3) 10–80 (100) mm long and 1/6 as long to subequal in length to the blade; *blades* (1.1) 2.5–6.0 (11.5) cm long × (0.3) 1.0–4.0 (10.0) cm wide, wide-ovate to lanceolate and occasionally obscurely 3-lobed, cordate truncate to wide-cuneate at the base, acute acuminate to rounded at the apex, sparsely to densely pubescent on both surfaces, margins crenate-dentate to dentate-serrate or denticulate with 2 7 teeth cm, palmate veins 3–7 with one a pronounced midvein, conspicuously raised below and somewhat impressed above; *flowers* axillary and solitary or in terminal racemes, congested terminal spikes, or in leafless glomerate axillary spicate racemes in the upper half of the plant, pedicellate to nearly sessile, pedicels 0.1 5 (10) mm long, subtended by leaves and/or stipules or a bifid bract derived from stipules, usually open for only a few hours; *involucel* of 3 bracteoles, 2–18 mm long × 0.2 5 mm wide, distinct, appressed, and free or adnate basally to the calyx, half as long as or subequal to the calyx, deltate-cordiform to lanceolate or linear, pubescent, occasionally ciliate; *calyx* in bud often strongly 5-angled, usually densely pubescent, 2.8–15 mm measured from pedicel to lobe-apex at anthesis, somewhat accrescent in fruit, sepals united 1/5 to 3 5 their length, lobes (1.5) 4–12 mm long × (1.5) 4–7 (12) mm wide in flower and fruit and deltoid to narrowly triangular, acute, acuminate to subcuspidate at the apex, erect, spreading, or incurved in fruit, internal lobe surface with minute arachnoid hairs, with 3–5 (10) subparallel veins lobe; *nectaries* 5, indistinct, consisting of zones of glandular hairs on the calyx below the petal-claws; *petals* 5 (rarely 6), 2.0 23 mm long × 1.5 15 mm wide and infrequently subequal to the calyx-lobes or exceeding them by as much as 8 mm, distinct, yellow or yellow-orange to pale orange, asymmetrically obovate and usually emarginate or unequally cleft, imbricate in bud with a basal non-auriculate yellow or rarely red claw 0.5 2 mm long with ciliate or bearded margins, corolla campanulate, wide-campanulate, or rotate at anthesis, rarely cleistogamous, confluent with the staminal column at the base producing an "ovary cup"; *androecium* with (5) 16 50 (111) 5-ranked or unranked monadelphous stamens, column shorter than the petals and matching them in color, the dorsifixed extrorse terminal anthers with valves oriented 180° after dehiscence,

the single locule partially divided by an incomplete septum, free portion of the filaments 0.5–1.0 mm long, filament-tube 1–7 mm in height, sparsely to moderately pubescent or glabrous; *gynoecium* with a single glabrous style branching halfway from its base into 5–18 branches equal in number to the carpels; *stigmas* terminal, subglobose, hemispherical, or unexpanded, generally papillate, yellow or rarely magenta; *carpels* in a single discoid whorl attached by their proximal margins to a central apically expanded columella, subtended by a thin carpocrater; *ovules* one in each carpel, ascending, attached to the columella below the carpel notch; *fruit* an oblate or discoid schizocarp 3–11 mm in diameter (including ornamentation), exposed or enclosed by the calyx, green or bright rose-red drying to pale, tan reddish brown to dark brown at maturity, readily or tardily shed from the shrunken columella and calyx at maturity; *mericarps* 5–18, completely to partially dehiscent or indehiscent, free from one another, laterally compressed and wedge-shaped with angular or rounded margins, 1.0–6 mm tall × 1.0–6 mm long × 0.8–2.0 mm wide including ornamentation, sparsely to densely pubescent on the apical, apical-distal, and lateral surfaces near the margins with simple and/or stellate hairs, rarely glabrous, with a conspicuous proximal notch, lateral faces smooth to radially ribbed, thin and chartaceous to leathery or firm and woody, the apical-distal-basal surface with or without a raised medial line, unornamented or more frequently with one to three apical mucros or cusps 0.1–2.3 mm long that are vertically cleft or entire, rarely the distal margins prolonged into short wings, internal surface smooth, lustrous, and glabrous, with or without a small intrusive proximal-apical endoglossum; *seeds* solitary in each mericarp, 1.0–2.5 mm long × 1–3.0 mm in height × 0.6–1.5 mm wide, ascending, incompletely filling the chamber at maturity, somewhat asymmetrically reniform or rarely narrowly elongated, glabrous, with a thick gray red-brown or black seed-coat, with or without a medial distal-apical sulcus; *chromosome-number*: $x = 6$, $2n = 12, 18, 24, 48$; *pollen* spheroidal to oblate, (36) 60–90 (108) μm in diameter, echinate with spines (2.3) 4–7 (10) μm, operculate and panporate with (4) 6–15 (35) apertures.

DISTRIBUTION.

Central United States south through Central America and the Caribbean to San Juan, Córdoba, and Buenos Aires, Argentina.

Widely introduced in the Old World Tropics especially in coastal regions, especially common in India and Australia, and probably indigenous in the latter.

KEY TO TAXA OF MALVASTRUM

1. Mericarps unornamented or with 1 proximal-apical mucro < 0.2 mm long ..... (2)
   2. Mericarps completely dehiscent into 2 valves with rounded margins; flowers solitary axillary; all leaves narrowly lanceolate, at least 3 times longer than wide; central United States (Section *Sidopsis*) ..... 1. *M. hispidum*
   2. Mericarps not separating into 2 valves, with angled margins; flowers in mature plants in terminal spikes or congested axillary spicate racemes; leaves ovate, sometimes narrower at branch apices, usually 1–2 times longer than wide; widespread ..... (3)
      3. Apical surface of mericarp with stellate hairs only; lateral faces of pericarp thin and fragile; flowers in leafless axillary and/or terminal congested spicate racemes <3 cm long at maturity; Argentina and Bolivia (Section *Interruptum*) ..... (4)
         4. Mericarps 7–10, 1.0–1.5 mm in height × 1.0–1.5 mm in length × 1.4 mm in width, stamens 5–7 ..... 2. *M. spiciflorum*
         4. Mericarps 10–12, 1.9–2.0 mm in height × 2.0–2.2 mm in length × 0.8–1.0 mm in width, stamens 20–27 ..... 3. *M. interruptum*
      3. Apical surface of mericarp with some simple hairs; lateral faces of pericarp firm; flowers in basally leafy terminal racemes or spikes commonly >3 cm long at maturity; widespread ..... (5)
         5. Vesture of vegetative parts of 3–5-rayed appressed stellate hairs; inflorescence of solitary axillary flowers or a congested or loose terminal spike 1–2 cm long or infrequently longer; mostly Caribbean (Section *Corchorifolium*) ..... 14. *M. corchorifolium*
         5. Vesture of vegetative parts of 5–12-rayed, often tufted stellate hairs; inflorescence a raceme or terminal spike usually >3 cm long; widespread (Section *Americanum*) ..... (6)

6. Mericarps 7–8, the simple hairs of the apical surface confined to the proximal portion, the pericarp indehiscent; northern Queensland, Australia .... 5. *M. chillagoense*

6. Mericarps 9–18, the apical surface rather densely pubescent throughout with simple or both simple and stellate hairs, pericarp usually incompletely dehiscent along basal-medial line; widespread (7)

7. Apical surface of mericarp with erect and appressed simple hairs only; bracteoles subequal to the calyx in flower; widespread ....4a. *M. americanum* var. *americanum*

7. Apical surface of mericarp with two zones of hairs: distal zone composed of appressed 5–10-rayed stellate hairs and proximal zone of erect simple hairs; bracteoles exceeding the calyx lobes in flower; eastern Australia .... 4b. *M. americanum* var. *stellatum*

1. Mericarps with 1–3 cusps >0.2 mm long ..... (8)

8. Apical mucro of mericarp if present set at the proximal margin; filament-tube pubescent; vesture of the stems of 4 8-rayed radially symmetric hairs; Western Hemisphere ..... (9)

9. Distal pericarp margins never winged; mericarps 9 13, bifid floral bracts often present; inflorescence usually racemose (Section *Tomentosum*) ..... (10)

10. Mericarp with a proximal-apical mucro or cusp 0.1–1 mm long, total height 2–3 mm, pericarp dehiscent at the proximal-apical margin; bracteoles linear, free from the calyx; South America ..... (11)

11. Distal cusps of mericarp 0.8–2 mm long, proximal cusp 0.1–0.5 mm long; calyx lobes patent in fruit; lateral faces of pericarp usually strongly ribbed, the vesture of the apical surface of symmetrical stellate hairs; seeds with a distal-apical sulcus; Brazil, Ecuador, Peru, Venezuela .... 6a. *M. tomentosum* subsp. *tomentosum*

11. Distal cusps of mericarp 0.3–0.7 mm long, proximal cusp 0.05–0.3 mm long; calyx lobes incurved or slightly spreading in fruit; lateral faces of pericarp smooth except for a few basal ribs, the vesture of

the apical surface of asymmetrical stellate hairs or a mixture of simple and stellate hairs; seeds without a sulcus; Ecuador, Peru ..... (12)

12. Vesture of apical surface of mericarp of asymmetrical stellate hairs, the lateral surface pubescent distally; petals 6–7 mm long and 3–5 mm wide; bifid floral bracts absent; Prov. Azuay, Ecuador ..... 6b. *M. tomentosum* subsp. *pautense*

12. Vesture of apical surfce of mericarp of simple hairs with a few minute stellate hairs, the lateral surfaces glabrous; petals 10–13 mm long and 9–10 mm wide; bifid floral bracts usually present; northern Peru ..... 7. *M. scoparioides*

10. Mericarp lacking a proximal apical cusp or with a mucro <0.1 mm long, total height 1.8–2.0 mm, pericarp indehiscent at the proximal-apical margin; bracteoles lanceolate, adnate to the calyx basally for 1–3 mm; Arizona to Nicaragua ..... (13)

13. (10) Distal margins of lateral surfaces of mericarp with dense brushlike simple hairs; stem vesture of 2–6-rayed stellate hairs mixed with minute erect simple hairs; Guatemala, Honduras, Nicaragua ..... 8. *M. guatemalense*

13. Distal margins of lateral surfaces of mericarp glabrous or sparsely pubescent; stem vesture of 4–8-rayed stellate hairs; Arizona to Oaxaca, Mexico .. (14)

14. Mericarp woody, dull, apical surface densely pubescent; lateral faces of pericarp ribbed; Arizona, northwestern and central Mexico .. (15)

15. Distal cusps of mericarp 0.5–1.5 mm long; lateral faces of pericarp distinctly ribbed; calyx-lobes patent in fruit, external surface sparsely pubescent; mericarps exposed; stigmas exserted 1.0–1.5 mm beyond anther cluster; Arizona and northern Mexico ..... 9a. *M. bicuspidatum* subsp. *bicuspidatum*

15. Distal cusps of mericarp 0.1–1 mm long; lateral faces of pericarp scarcely ribbed; calyx-lobes slightly spreading in fruit, external surface

densely pubescent; mericarps enclosed by the calyx; stigmas exserted <1.0 mm beyond anther cluster; central high plateau of Mexico ..... 9b. *M. bicuspidatum* subsp. *campanulatum.*

14. Mericarp leathery or chitinous, somewhat lustrous, apical surface sparsely pubescent or glabrous; lateral faces of pericarp smooth or inconspicuously ribbed toward margins; central and southern Mexico ..... (16)

16. Mericarp not plump, the apical surface with stellate hairs <0.5 mm long; endoglossum present; petals 10–14 mm long; leaves paler beneath; Oaxaca, Puebla .... 9c. *M. bicuspidatum* subsp. *oaxacanum*

16. Mericarp plump, the apical surface with a few erect simple or 2–3-rayed stellate hairs 0.5–1 mm long or glabrous; endoglossum absent; petals 7–10 mm long; leaves concolorous; Jalisco to Morelos ..... (17)

17. Mericarps pubescent .. 9d. *M. bicuspidatum* subsp. *tumidum* var. *tumidum*

17. Mericarps glabrous .... 9e. *M. bicuspidatum* subsp. *tumidum* var. *glabrum*

9. Distal pericarp margins briefly winged; mericarps 11 18, bifid floral bracts absent; flowers solitary, axillary (Section *Amblyphyllum*) ..... (18)

18. Petals 17 23 mm long × 12–15 mm wide, exceeding the calyx by 4 5 mm; stigmas exceeding the anthers by 3 mm; leaf blades acute to acuminate; Bolivia .... 10. *M. grandiflorum*

18. Petals 6–12 mm long × 3.5–4.5 mm wide, exceeding the calyx by 2 mm; stigmas subequal to anthers; leafblades obtuse; Bolivia, Paraguay, Argentina .... 11. *M. amblyphyllum*

8. Apical mucro or cusp of mericarp set halfway between the proximal and distal margins; filament-tube glabrous or less frequently sparsely pubescent; vesture of the

stems of sub-lepidote 6–10-rayed or appressed 2–4-rayed stellate hairs occasionally mixed with simple hairs, the 4-rayed hairs distinctly bilateral; widespread ..... (19)

19. Endoglossum present but rudimentary; stamen column sparsely pubescent; cusps on mature carpels usually <0.2 mm long; bifid floral bracts present (Section *Corchorifolium*) ..... 14. *M. corchorifolium*

19. Endoglossum absent; stamen column glabrous; cusps on mature carpels >0.2 mm long; bifid floral bracts usually absent (Section *Malvastrum*) ..... (20)

20. Vesture of vegetative parts of sub-lepidote 6 10-rayed stellate hairs usually with basally united rays; mericarp with a prominent medial-apical cusp 1.5–2.3 mm long and 2 contiguous flattened obtuse cusps at the distal margin; Texas, U.S.A. ..12. *M. aurantiacum*

20. Vesture of vegetative parts composed of simple or 2–4-rayed bilateral stellate hairs; mericarp with a prominent or small medial-apical cusp 0.2–1.2 mm long and 2 divergent pointed cusps at the distal margin; widespread ..... (21)

21. Mericarps 1.5–2.0 mm in height × 2.0 mm in length including ornamentation; proximal cusp 0.2–0.4 mm long and distal-apical cusps 0.1–0.2 mm long; bifid floral bracts often present; south-central Brazil ..... 13c. *M. coromandelianum* subsp. *fryxellii*

21. Mericarps 2.4–4.5 mm in height × 3–4 mm in length including ornamentation; proximal cusp 1.0–2.0 mm long and distal-apical cusps 0.3–1 mm long; bifid bracts absent; widespread ..... (22)

22. (21) Annual or perennial herb generally with several main stems 0.2–1 m tall in age; flowers solitary axillary, somewhat apically congested in age; vesture of upper leaf surface usually of simple hairs, less frequently of stellate hairs; widespread ..... 13a. *M. coromandelianum* subsp. *coromandelianum*

22. Mostly perennial herbs with single main stem 0.3–

1.5 m tall in age; flowers in congested, glomerate axillary racemes ca. 1 cm long; vesture of upper leaf surface of bilateral 4-rayed stellate hairs; Argentina, Bolivia, Galápagos .... 13b. *M. coromandelianum* subsp. *capitato-spicatum*

Summary of taxa of *Malvastrum* A. Gray
(numbers correspond to text)

Malvastrum sect. *Sidopsis* (Rydberg) S. R. Hill
1. *Malvastrum hispidum* (Pursh) Hochreutiner
Malvastrum sect. *Interruptum* S. R. Hill
2. *Malvastrum spiciflorum* (E. Hassler) A. Krapovickas
3. *Malvastrum interruptum* K. Schumann in Martius
Malvastrum sect. *Americanum* S. R. Hill
4a. *Malvastrum americanum* (Linnaeus) Torrey in Emory var. *americanum*
4b. *Malvastrum americanum* var. *stellatum* S. R. Hill
5. *Malvastrum chillagoense* K. Domin
Malvastrum sect. *Tomentosum* S. R. Hill
6a. *Malvastrum tomentosum* (Linnaeus) S. R. Hill subsp. *tomentosum*
6b. *Malvastrum tomentosum* subsp. *pautense* S. R. Hill
7. *Malvastrum scoparioides* E. Ulbrich
8. *Malvastrum guatemalense* Standley & Steyermark
9a. *Malvastrum bicuspidatum* (S. Watson) Rose subsp. *bicuspidatum*
9b. *Malvastrum bicuspidatum* subsp. *campanulatum* S. R. Hill
9c. *Malvastrum bicuspidatum* subsp. *oaxacanum* S. R. Hill
9d. *Malvastrum bicuspidatum* subsp. *tumidum* S. R. Hill var. *tumidum*
9e. *Malvastrum bicuspidatum* subsp. *tumidum* var. *glabrum* S. R. Hill
Malvastrum sect. *Amblyphyllum* S. R. Hill
10. *Malvastrum grandiflorum* A. Krapovickas
11. *Malvastrum amblyphyllum* R. E. Fries
Malvastrum sect. *Malvastrum*, emend. S. R. Hill
12. *Malvastrum aurantiacum* (Scheele) Walpers
13a. *Malvastrum coromandelianum* (Linnaeus) Garcke subsp. *coromandelianum*

13b. *Malvastrum coromandelianum* subsp. *capitato-spicatum* (O. Kuntze) S. R. Hill

13c. *Malvastrum coromandelianum* subsp. *fryxellii* S. R. Hill

Malvastrum sect. *Corchorifolium* S. R. Hill

14. *Malvastrum corchorifolium* (Desrousseaux in Lamarck) Britton ex Small

TREATMENT OF INDIVIDUAL TAXA

Section 1. *Sidopsis*

Malvastrum sectio **Sidopsis** (Rydberg) S. R. Hill, comb. et stat. nov.

Sidopsis Rydberg, Fl. Pr. Pl. Cent. N. Amer.: 541. 1932, pro genere. TYPE species: *S. hispida* (Pursh) Rydberg [= *Malvastrum hispidum* (Pursh) Hochreutiner].

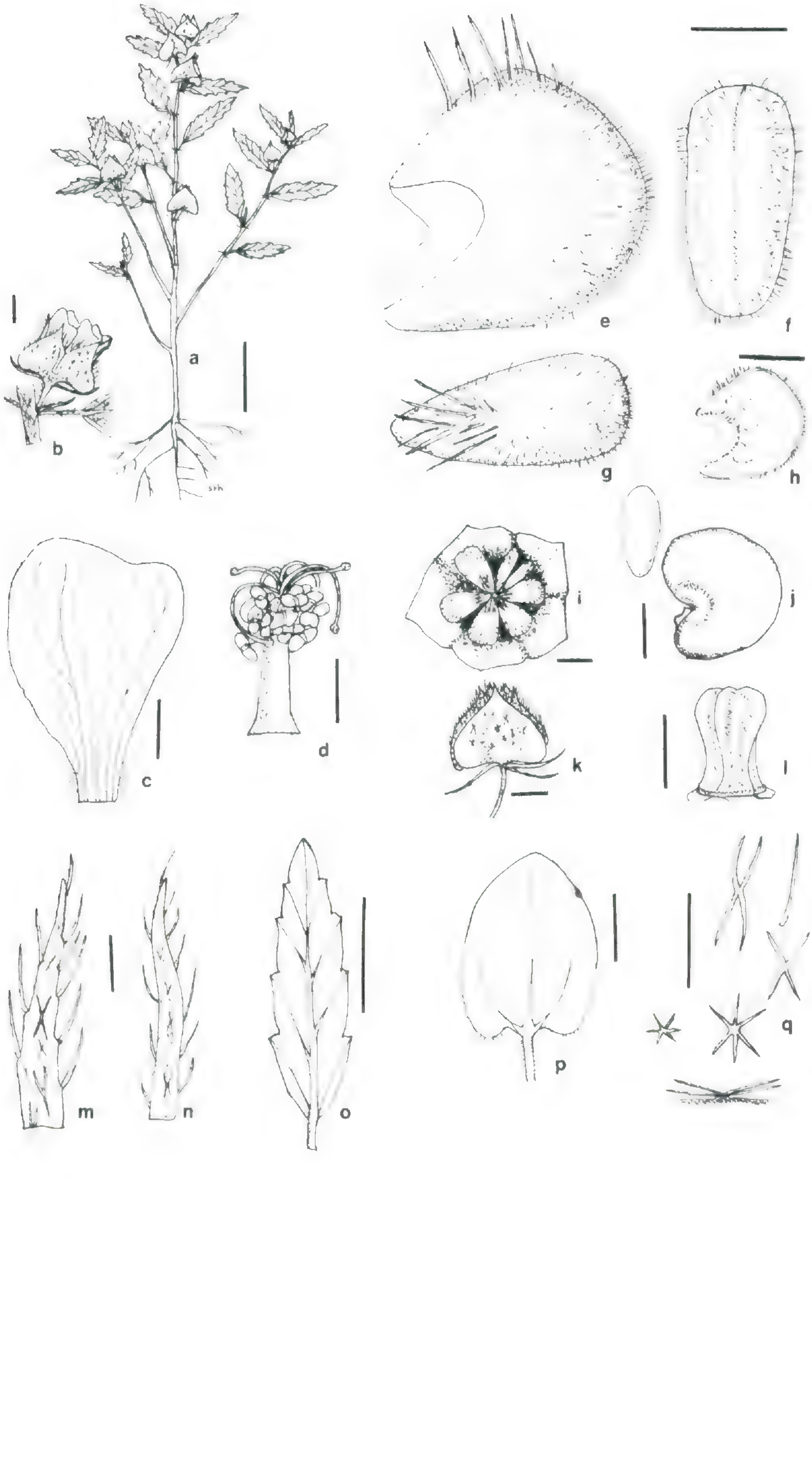
The solitary axillary occasionally cleistogamous flowers, completely dehiscent thin-walled unornamented mericarps (follicules), lack of an endoglossum and bifid floral bracts, glabrous filament tube, and 11–15 aperturate pollen characterize the section *Sidopsis*.

1. **Malvastrum hispidum** (Pursh) Hochreutiner, Annuaire Conserv. Jard. Bot. Genève 20: 129. 1917. Fig. 19.

Sida hispida Pursh, Fl. Amer. Sept.: 452. 1814. TYPE: "In sandy plains of Georgia. *Lyon*", apparently not preserved. Bates (1967a, p. 25) chose Pursh's description as the lectotype. *Malveopsis hispida* (Pursh) O. Kuntze, Rev. Gen. **1**: 72. 1891. *Sidopsis hispida* (Pursh) Rydberg, Fl. Pr. Pl. Centr. N. Am.: 541. 1932.

Malvastrum angustum A. Gray, Mem. Amer. Acad. Arts ser. 2, **4**: 22, in adn. 1849. TYPE: Missouri: St. Louis, 1832. *Drummond s.n.* (LECTOTYPE: GH; ISOTYPES: BM, K) chosen by Bates (1967a, p. 26). *Malva perpusilla* Nuttall ex A. Gray, Mem. Amer. Acad. Arts. ser. 2, **4**: 22, in adn. 1849, nomen nudum, pro syn. A manuscript name on a specimen collected near the Red River, *Nuttall s.n.* (NY!). *Sphaeralcea angusta* (A. Gray) Fernald, Rhodora **41**: 435. 1939.

Bushy-branched herbaceous annual (5) 25–45 (60) cm tall; *main stem* 1–3.5 mm diam at base; *branches* (7) 15–20 (30) cm long towards the main stem base and gradually reduced above; *vesture* of overlapping 4 (6)-rayed bilateral appressed, usually tuberculate-based, stellate hairs (0.5) 0.9–1.2 (2.2) mm diam longitudinal to the axis, scarcely or tardily shed in age; *cotyledons* 7 mm long × 6 mm wide, petiole 4 mm long, ovate, cordate at the base and rounded to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slightly retuse at the apex; *stipules* (2) 3–5 (7) mm long × 0.2–0.3 (0.5) mm wide, linear to linear-lanceolate to narrowly subulate; *petioles* (3) 5–10 (13) mm long; *blades* 3.1–3.9 (5)× longer than the petioles, (15) 25–35 (55) mm long × (3) 5–9 (15) mm wide and not conspicuously reduced above, lanceolate to linear-lanceolate and unlobed, base narrowly rounded to nearly cuneate, apex acute to briefly cuspidate, margins sparsely serrate-dentate with 2–2.5 teeth/cm, average midstem blade (2.8) 3.1–3.6 (8.3)× longer than wide, vesture of the adaxial surface of scattered appressed non-overlapping (2) 4 (6)-rayed slightly bilateral hairs (0.2) 0.5–0.8 (1.1) mm diam directed towards the vein apices, often reduced to small simple hairs at the margins, vesture of the abaxial surface of similar (4) 6 (8)-rayed appressed hairs; *flowers* solitary in axils of upper main stem and branch leaves and stipules, infrequently in 2–3-flowered reduced branches near the apex; bifid *floral bracts* lacking; *pedicels* 2–4 (10, rarely to 20) mm long in flower increasing to 5 8 (17, rarely to 25) mm in fruit; *involucel* of 3 narrowly lanceolate to linear or subfalcate bracteoles (2.6) 4–6.8 mm long × 0.3–0.6 mm wide free of the calyx or less frequently adnate in the basal 0.5–1.0 mm; *calyx* united 2/5 to 1/2 its length, (2.8) 5–7.2 mm from pedicel to lobe apex in flower increasing to (6) 8–10 (12.5) mm in fruit, broadly campanulate and distinctly plicate-angular due to the prolonged reniform-auriculate lobe bases, lobes (1.5) 4–5 mm long × (2) 4–5 mm wide at anthesis increasing to 7–10 mm × 7–10 (12) mm in fruit, abaxial vesture of overlapping 4–6-rayed stellate hairs 0.3–1.5 mm diam and with simple or 2-rayed marginal hairs 0.8–1.1 mm long, adaxial surface of lobes minutely puberulent with minute arachnoid hairs; *corolla* yellow to pale yellow-orange, petals asymmetrically obovate and briefly lobed, (2.8) 3.5–4.5 mm long ×

Figure 19. *Malvastrum hispidum*. a. Habit, scale = 5 cm. b. Flower, scale = 2 mm. c. Petal, scale = 1 mm. d. Stamens, styles, and stigmas, scale = 1 mm. e–g. Mericarp, lateral, distal, and apical views, scale = 1 mm. h. Mericarp valve, internal surface, scale = 2 mm. i. Fruit, apical view, scale = 2 mm. j. Seed, apical and lateral views, scale = 1 mm. k. Calyx in fruit, lateral views, scale = 5 mm. l. Columella, lateral view, carpocrater nearly absent, scale = 1 mm. m. Stipule, abaxial surface, scale = 1 mm. n .Bracteole, abaxial surface, scale = 1 mm. o. Leaf, abaxial surface, scale = 1 cm. p. Cotyledon, scale = 2 mm. q. Hair types, leaf and stem, scale = 1 mm. (a,n,o.q from *Bates 2686;* b–d from *Eggert 1282;* *e*–h,j,l from *Horr & Franklin E180;* i. from *Palmer 66567;* k,m from *Bates 2705;* p from *Rodin s.n.*).

Figure 20. Distribution of *Malvastrum hispidum*.

(1.5) 2.5–3.5 mm wide, campanulate or unexpanded, subequal to the calyx or exceeding it by 0.5–1.0 mm, claws ciliate with few (3–5) simple hairs 0.4 mm long; *androecium* with 8 13 (16) stamens, filament tube (1.0) 1.4–1.6 mm long, glabrous, free portion of filaments 0.2 0.5 mm long; *gynoecium* with 5–6 carpels, style branching 1.5 mm above the columella, each branch terminated by an expanded globose papillose stigma recurved into the anther cluster before and after anthesis; *schizocarps* (5.6) 7 8 mm diam; *mericarps* (follicules) 5 6, (2.6) 3.0 3.5 mm in height × (2.6) 3.0 –3.5 mm in length × 1.5 mm in width, separate at maturity, unornamented, margins rounded and lateral surfaces unribbed, apical-

distal-basal surface with a medial line, pubescent nearly throughout with minute simple hairs 0.1 mm long perpendicular to the pericarp surface and elongated flexible erect simple hairs 0.2 1.0 mm long restricted to the proximal-apical surface, pericarp thin and somewhat hyaline to chartaceous throughout, completely dehiscent loculicidally at maturity and separating into two valves, endoglossum lacking; *seeds* 2.1 2.5 mm in height × 2.0 2.5 mm in length × 1.3–1.5 mm in width; *chromosome number : n* = 18; *pollen* 56–79 (60) μm diam, echinae 3.6 3.8 μm, apertures 11 15, usually 12.

DISTRIBUTION. (Fig. 20) Temperate North America, central portion of the United States from Illinois and Iowa in the north (also reported from Nebraska), to Arkansas and Oklahoma in the south (reported in Tallipoosa Co., Alabama), east to Kentucky and Tennessee, and west to Kansas, with its greatest frequency in Missouri, at an altitude of 150 500 m, occurring in full sun or partial shade in the vicinity of limestone outcrops, rocky prairies, and alluvial soils.

PHENOLOGY AND REPRODUCTIVE BIOLOGY. Flowering from early August through to late September, infrequently as early as mid-June and July. Plants transplanted from Missouri (*Hill 4533*) confirmed Bates' observations (1967a) that the flowers open in the late morning and early afternoon for a brief period (11 AM 2 PM local time) or often do not open at all, and so are functionally cleistogamous. The anthers dehisce before the flowers open and the stigmas are covered with pollen as the petals expand. Therefore the fruits seem to be nearly if not always produced by autogamy. Flower emasculation was not attempted. No pollinators are known.

The plants and fruits mature rather rapidly and the entire life cycle is often completed in three months, perhaps as an adaptation to the temperate environment.

DISCUSSION. I have chosen to follow Bates (1967a) in retaining this species in *Malvastrum*. While a case can be made for its retention in the monotypic genus *Sidopsis* because of its completely dehiscent mericarps, the genus would differ from *Malvastrum* only by the single character. Its diagnostic characters, particularly its chromosome number, coincide with those diagnostic characters in the other species of *Malvastrum*, but the problem remains that the species has no close relatives in the genus. Most of the character states that separate *M. hispidum* from the other species, e.g. the small flowers, annual habit, and disjunct range, are viewed as derived.

Specimens annotated *Sida hispida* Pursh from Georgia have been located at OXF and PH, part of the Beyrich Herbarium. The script is not Pursh's and Lyon is not cited. However, since these are the only specimens known bearing this name, and since they are actually *Sida carpinifolia* L. f. there is still some doubt in my mind that the name has been correctly applied.

Except to a limited extent in leaf width, there is little variation discernible within the species. The small population sizes and autogamous reproduction have further limited any influx of new variation into the gene pool.

REPRESENTATIVE SPECIMENS: **United States**. ARKANSAS, Boone Co., Harrison, *Palmer 6910* (GH, US); ILLINOIS, La Salle Co., Rock Island, *Parry s.n.* (BH, BKL, BUF, F, UC, US, VT); KANSAS, Bourbon Co., *Bates 2702* (BH, GH); 7 mi S of Uniontown, *Horr & Franklin E180* (SMU, US); Geary Co., NE corner of county, *Gates 17506* (F); Jewell Co., near Lovewell, *Tolstead 41996* (UC); Ness Co., prairie, *Hitchcock 44a* (GH, US); Osborne Co., Osborne, *Popenoe s.n.* (US); Pottawatomie Co., *Norton s.n.* (US); Riley Co., Manhattan, *Kellerman 367* (F); Trego Co., *Rodin s.n.* (F); KENTUCKY, Christian Co., S of Crofton, *Braun 3526* (US), Clark Co., Boone Creek above Grimes Mill, *Beckett 808* (GH), Jessamine Co., Hwy. 33, 0.3 mi E of Hwy. 68, *Bates 2705* (BH, GH, pf), Logan Co., near Russellville, *Braun 3538* (US), Mercer Co., Burgin, *King 186* (F, US); Warren Co., 12 mi W of Bowling Green, *Deam & Deam 60004* (F); Woodford Co., Hwy. 33, 0.8 mi W of Jessamine Co. line, *Bates 2704* (BH, GH, US); MISSOURI, Bates Co., 2.5 mi S of Butler, *Steyermark 21320* (F); Caldwell Co., Long Creek, 1.5 mi S of Kingston, *Steyermark 6062* (F); Callaway Co., Hwy. AA, 1 mi E of Hwy. 54, *Bates 2688* (BH, GH, US); Cass Co., 3.5 mi W of Peculiar, *Steyermark 5742* (F); Cedar Co., 0.5 mi S of Wagoner, *Steyermark 85798* (GA); Cooper Co., 2 mi NE of Clifton City, *Steyermark 21809* (F); Dallas Co., 3.5 mi S of Buffalo, *Steyermark 24159* (DAO, F); Greene Co., Valley Mill near Springfield, *Standley 8987* (US); Jackson Co., 1.3 mi E of Greenwood, *Bates 2691* (BH, GH, US); *Mackenzie s.n.* (VT); Jasper Co., Webb City, *Bush 9068* (GH); Jefferson Co., NW of Pevely, *Steyermark 4460* (F); Johnson Co., 1 mi W of Fayetteville, *Palmer 66567* (SMU); Laclede Co., Lebanon, Wire Road, *Moore 78* (F); Lafayette Co., 1 mi N of Chapel Hill, *Steyermark 24683a* (F); Lincoln Co., Cuivre River State Park, *Hill 4533* (srh); same locality, *Bates 2686* (BH, pf, TEX, US); McDonald Co., 3 mi E of Powell, *Palmer 61007* (SMU); Moniteau Co., between Kliever and Bacon, *Steyermark 24767* (F); Montgomery Co., E of Loutre River, *Steyermark 15893* (US); Pettis Co., 1.5 mi SW of Lookout, *Steyermark 21478* (F); Pike Co., *Peck s.n.* (F); Ralls Co., 1 mi N of Spaulding, *Steyermark 25711* (F); St. Charles Co., Alton (Allentown), *Letterman s.n.* (DAO, F, US); St. Claire Co., E side of Osage River, *Steyermark 24343* (F); St. Louis Co., St. Louis, *Engelmann s.n.* (F, G, US); Saline Co., 3 mi SW of Ridge Praire, *Steyermark 21555* (F); Stone Co., Galena, *Palmer 4637* (US); OKLAHOMA, Cherokee Co., 1.7 mi NE of Cookson, *Wallis 7989* (SMU); Johnston Co., Tishomingo, *Palmer 6491* (BH, UC, US); Osage Co., 7 mi N of Foraker, *Waterfall 13160* (GH); Sequoyah Co., 6 mi NE of Gore, *Wallis 7709* (SMU); TENNESSEE, Davidson Co., near Nashville, *Gattinger 367* (CU, F, G, PH, US, VT); Rutherford Co., La Vergne, *Svenson 9362* (BKL, GH, UC); Williamson Co., Sneed Rd.

towards Harpeth River, *Kral 28998* (MICH); Wilson Co., Gladeville, *Demaree 46345* (SMU).

Section 2. *Interruptum*

Malvastrum sectio **Interruptum** S. R. Hill, *sect. nov.*

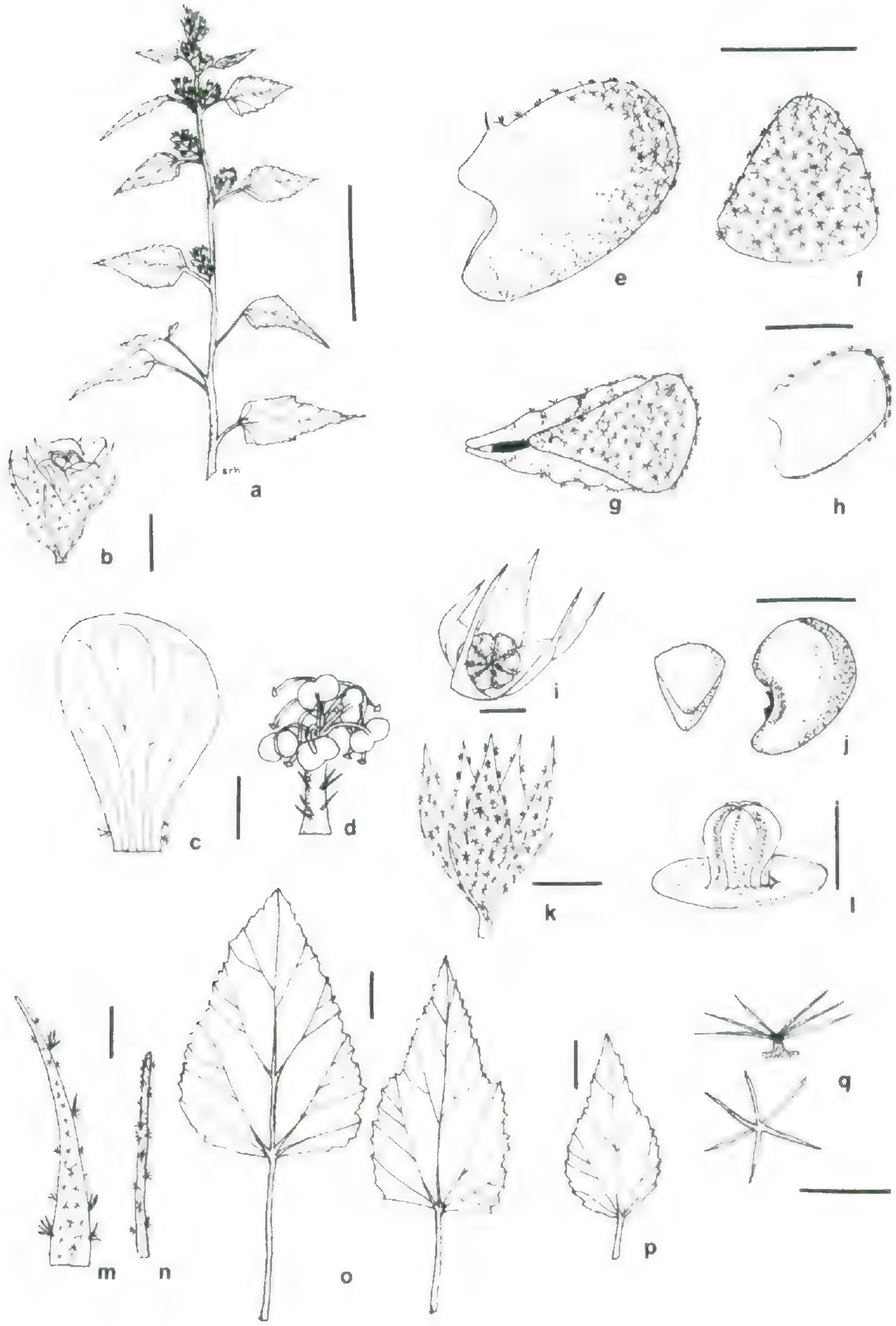
Carpella matura 7–12, indehiscentia, muris lateralibus tenuibus, pilis stellatis solum, inornata vel mucrone proximali-apicali singulo minuto minore quam 0.2 mm longitudine, marginibus pericarpium angulatis, endoglosso nullo; stamina 5–27, columna staminali subglabra; flores in racemis spicatis congestis aphyllis axillaribus vel terminalibus minoribus quam 3 cm longitudine; bracteolae involucelli calyce liberae; bracteae florales bifidae plerumque nullae; pili caulini interdum stipitati; pollinis grana aperturis 4-11. Typus: *Malvastrum interruptum* K. Schumann.

The glomerate axillary and terminal spikes, indehiscent thin-walled and disintegrating unornamented mericarps, the lack of an endoglossum and bifid floral bracts, sparsely pubescent filament tube, and 4 11 aperturate pollen characterize the section *Interruptum.*

2. **Malvastrum spiciflorum** (E. Hassler) A. Krapovickas, Darwiniana **10** (4): 634, in textu, 1954. Fig. 21, 22.

Malvastrum pentandrum K. Schumann subsp. *spiciflorum* E. Hassler, Feddes Repert. Spec. Nov. Regni Veg. 23: 495. 1913. TYPE: ARGENTINA. Tucumán: District of Tafí. Bajo de Anfama, alt 1600 m, 8 June 1906. *M. Lillo 5029.* (HOLOTYPE: G!, ISOTYPES: G!, LIL).

Herbaceous to suffruticose sparsely branched perennial or annual 0.6 1.2 m tall with a single *main stem* 3–5 (6) mm diam at base; *branches* 1 5 (25) cm long; stem *vesture* of (4) 5 8-rayed often tuberculate-stipitate stellate hairs (0.5) 1.0–2.0 mm diam, somewhat overlapping, tardily shed in age; *cotyledons* unknown; *stipules* (3) 6–8 mm long × 0.4–0.8 mm wide, reduced in the inflorescence, narrowly lanceolate to linear or subulate, subfalcate, long-acuminate; *petioles* (7) 20 35 mm long, shortest near the stem apex, borne at a 30°–60° angle to the stem above; *blades* 1.6–1.8 to 2.0–2.8× longer than the petioles on main stem and inflorescence-associated leaves respectively, 5 60 (70) mm long × (14) 20 30 (40) mm wide, average midstem blade (1.5) 1.8–2.2× longer than wide, triangular-ovate to ovate-lanceolate, unlobed or briefly 3-lobed half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the distance from the truncate to broadly rounded or wide-cuneate base, apex acute to long-acuminate, margin dentate to twice-dentate in lower leaves to denticulate in upper leaves with 3 6 teeth/cm, vesture of the adaxial surface of sparse to slightly overlapping simple to 2 6-rayed scarcely appressed hairs 0.5–1.0 mm diam, abaxial surface with similar but more dense (6) 10–12-rayed tufted stellate hairs; *flowers* at first solitary, axillary, later in congested axillary and terminal spicate racemes less than 2 cm long and generally shorter than the petioles of subtending leaves, flowers subtended by reduced leaves and their associated stipules or by reduced stipules alone, bifid *floral bracts* lacking; *pedicels* (0.5) 1.0–2.0 mm long and scarcely increasing in fruit; *involucel* of 3 linear bracteoles 2–3 mm long × 0.2–0.3 mm wide, completely free from the calyx; *calyx* united 1/5 to 1/4 its length, campanulate with slightly spreading to erect lobes, 3.5 4.0 mm long to 5–6 mm in fruit, lobes triangular, acuminate, 3.0–3.5 mm long × 1.5–2.0 mm wide in fruit, abaxial vesture of sparse tufted minute 6–10-rayed stellate hairs 0.05 0.3 mm diam, the largest on the margins of the lobes and conspicuous on the angles of the flower bud, adaxial lobe surface with a few minute arachnoid simple and stellate hairs on the apical 1/4 and marginally to the sinus; *corolla* yellow, petals asymmetric and unlobed, 3.0–3.5 (4.0) mm long × 2.0 mm wide, presumably campanulate to slightly spreading, subequal in length to the calyx, claws with 1 or 2 marginal stellate hairs 0.2 mm long; *androecium* with 5–6 (7) stamens, filament tube 1.0–1.4 mm long, subglabrous with 1–5 fine simple or 2–4-rayed stellate hairs similar to those of the petal claws, free portion of filaments 0.2–0.5 mm long; *gynoecium* with 7–8 (10) carpels, the style branching 1.5–2.0 mm above the columella, the branches usually recurved and subequal to the anthers, each stigma slightly expanded subhemi-

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Figure 21. *Malvastrum spiciflorum*. a. Habit, scale = 5 cm. b. Flower, scale = 2 mm. c. Petal, scale = 1 mm. d. Stamens, styles, and stigmas, scale = 1 mm. e.–g. Mericarp, lateral, distal, and apical views, scale = 1 mm. h. Mericarp, internal view, scale = 1 mm. i. Fruit, apical view, scale = 2 mm. j. Seed, apical and lateral view, scale = 1 mm. k. Calyx in fruit, lateral view, scale = 2 mm. l. Columella and carpocrater, scale = 0.5 mm. m. Stipule, abaxial surface, scale = 1 mm. o.–p. Leaves, basal to apical, line-scale = 1 cm. q. Stem hairs, line-scale = 0.5 mm. (a,o–p, from *Krapovickas, et al.* 22080; b–d, k, q from *Rodrigo 2293;* e–j, l, from *Lillo 5029*).

Figure 22. *Malvastrum spiciflorum* (holotype).

spherical and papillose; *schizocarps* 3.0 3.5 mm in diam; *mericarps* 7-8 (10), 1.0 1.5 mm in height × 1.0–1.5 mm in length × 1.4 mm in width, the portion below the hilum region of the seed often prolonged, conspicuously wider at the base than apex in distal profile, usually with a single proximal-apical mucro 0.5 0.1 mm long, lateral surfaces minutely granular in appearance, with inconspicuous ribs or reticulate rays more conspicuous at the distal and basal margins, vesture limited to the apical and distal surfaces, composed of minute 6–10-rayed stellate hairs 0.05 mm diam, occasionally a few proximal hairs bear prolonged rays to 0.1 mm in length, pericarp chartaceous throughout very thin and fragile over the seeds and soon disintegrating, a thin medial line visible on the basal portion of the distal surface, indehiscent but weakly sealed in the proximal-basal region, endoglossum lacking, mericarps readily detaching from the receptacle at maturity but tardily shed due to the obstructing calyx lobes; *seeds* 1.0 mm in height × 1.0 mm in length × 0.6-0.7 mm in width; *chromosome number:* $2n = 12$; *pollen* 35.8–59 (50) μm diam, echinae 2.3–4.0 μm, apertures 4–5.

DISTRIBUTION. (Fig. 23) Restricted to highland regions from Córdoba, Argentina in the south to La Paz, Bolivia in the north at elevations of 1600–2700 m, the higher elevations corresponding to the northern populations.

PHENOLOGY AND REPRODUCTIVE BIOLOGY. This species apparently flowers in March–June (local late summer and autumn). The few seeds planted in Texas did not germinate. The primary pollination mechanism is suspected to be self-pollination due to the small inconspicuous corolla and the reduced number of stamens that apparently release their pollen directly onto the stigmas.

DISCUSSION. *Malvastrum spiciflorum* strongly resembles *M. interruptum* at maturity and their ranges coincide. It is apparently local or very scarce throughout its range. This is the only diploid species of *Malvastrum* and so primitive generic characters have been sought here. It is apparent, however, that although *M. spiciflorum* is a diploid, many of its character states are derived or reduced when examined in the genus as a whole. Nevertheless, its distribution is thought to be relictual.

SPECIMENS EXAMINED: **Argentina.** CÓRDOBA: Dpto. Cruz del Eje, Río Pinto, *Rodrigo 2293* (NY); SALTA: Dpto. Chicoana, Cuesta del Obispo, San Martín, *Krapovickas et al. 22080* (F, GH, pf, UC, WIS);

La Zanja, *Krapovickas & Schinini 36055* (MARY, srh); TUCUMÁN: Bajo de Anfama, *Lillo 5029* (G); **Bolivia.** LA PAZ: Larecaja, Sorata, *Mandon 817?,* mixed with *M. interruptum,* (GH).

3. **Malvastrum interruptum** K. Schumann in Martius, Fl. Bras. **12**, 3: 272. 1891. TYPE: ARGENTINA. Córdoba: Dpto. Colón, Sierra Chica near Ascochinga, April 1871. *P. G. Lorentz 276* (LECTOTYPE: GOET!; ISOTYPES: G! US!) Fig. 24, 25

Malvastrum spicatum sensu A. Grisebach, Abh, Königl, Ges. Wiss. Göttingen **19**: 89. 1874, non A. Gray, 1849. Grisebach applied this name to several specimens including notably *Lorentz 276,* later the type of *M. interruptum.*

Suffruticose to sub-arborescent sparsely branched perennial herb (1.0) 1.5 2.5 (3.0) m tall with a stout single *main stem* 10 15 mm diam at base; *branches* few, 15 30 cm long on older plants; stem *vesture* of often tuberculate-stipitate 4-rayed stellate hairs 0.6 2.0 mm diam overlapping but not obscuring the stem surface, hairs persistent; *cotyledons* 6 7 mm long × 8 9 mm wide, wide-ovate, apex rounded, base subtruncate to broadly rounded; *stipules* 5 7 (9) mm long × 0.7 1.0 mm wide, narrowly-lanceolate to linear or subulate, subfalcate, long-acuminate; *petioles* (7) 16 30 (50) mm long shortest near stem apex, borne at a 30° 60° angle to the stem above; *blades* (1.2) 2.2 3.2 (3.7)× longer than the petioles, (25) 50 90 (125) mm long × (12) 25 40 (97) mm wide, average midstem blade 1.7 2.4× longer than wide, narrowly triangular-ovate or ovate-lanceolate to wide-ovate (in the earliest seedling leaves), upper surface concave and leaf thus appearing slightly cupped, unlobed or infrequently briefly 3-lobed 1/2 to 2/3 the distance from the broadly cuneate truncate to somewhat reniform-cordate base, apex acute, margin dentate to denticulate with 3 5 teeth/cm, nerves impressed and conspicuous above, vesture of the adaxial surface of overlapping but usually not dense 2 4 (6)-rayed stellate hairs 0.3 1.0 mm in diam the rays often directed marginally or apically, abaxial pubescence of usually more dense 10 12-rayed stellate hairs; *flowers* at first solitary in axils of upper main stem leaves, soon in several densely congested and apparently continuous axillary and terminal spicate racemes each less than 3 cm long, flowers subtended by highly reduced leaves and their associated stipules by stipules alone or less frequently by *floral bracts* divided 2/3 to 5/6 their length;

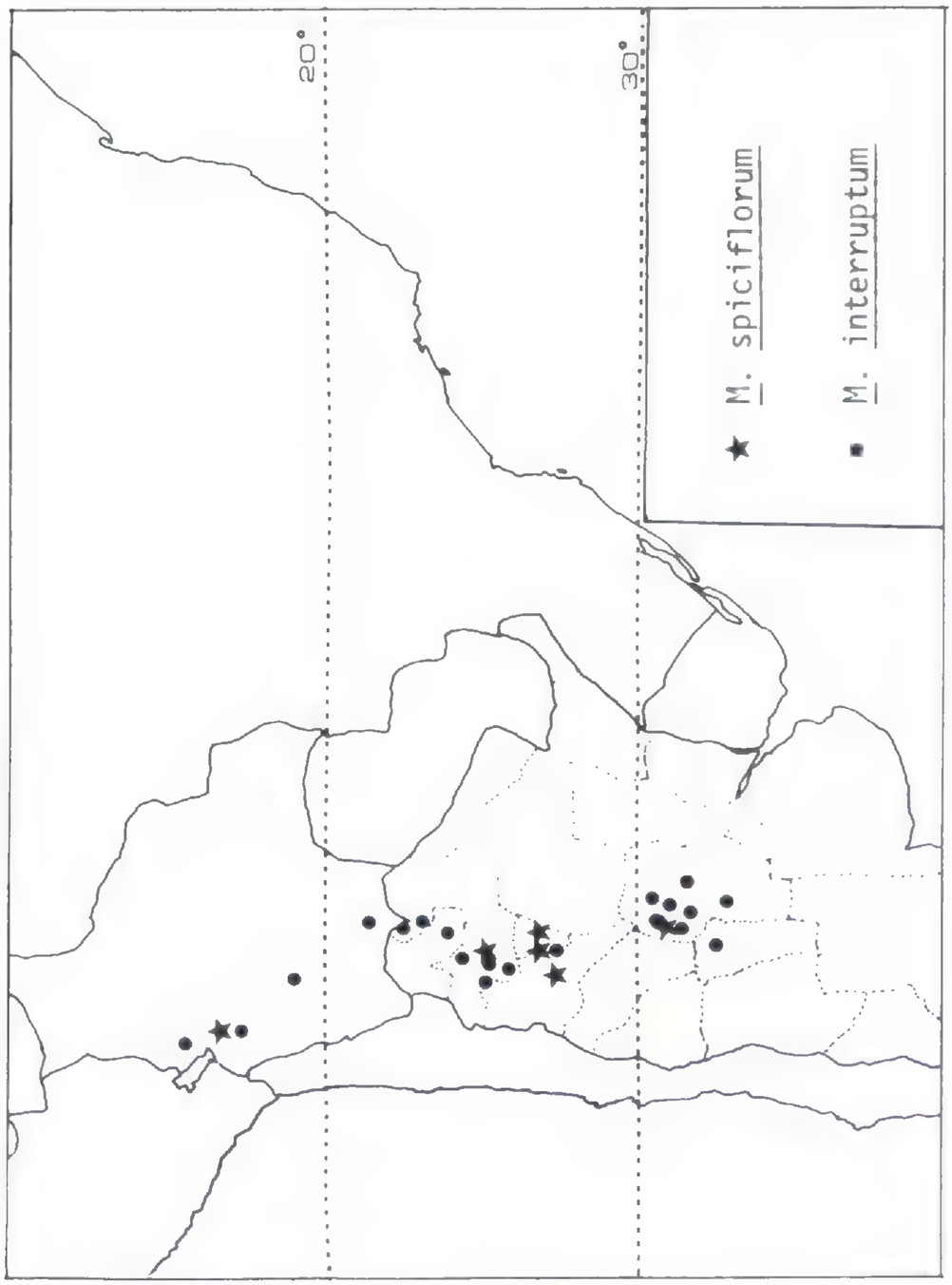
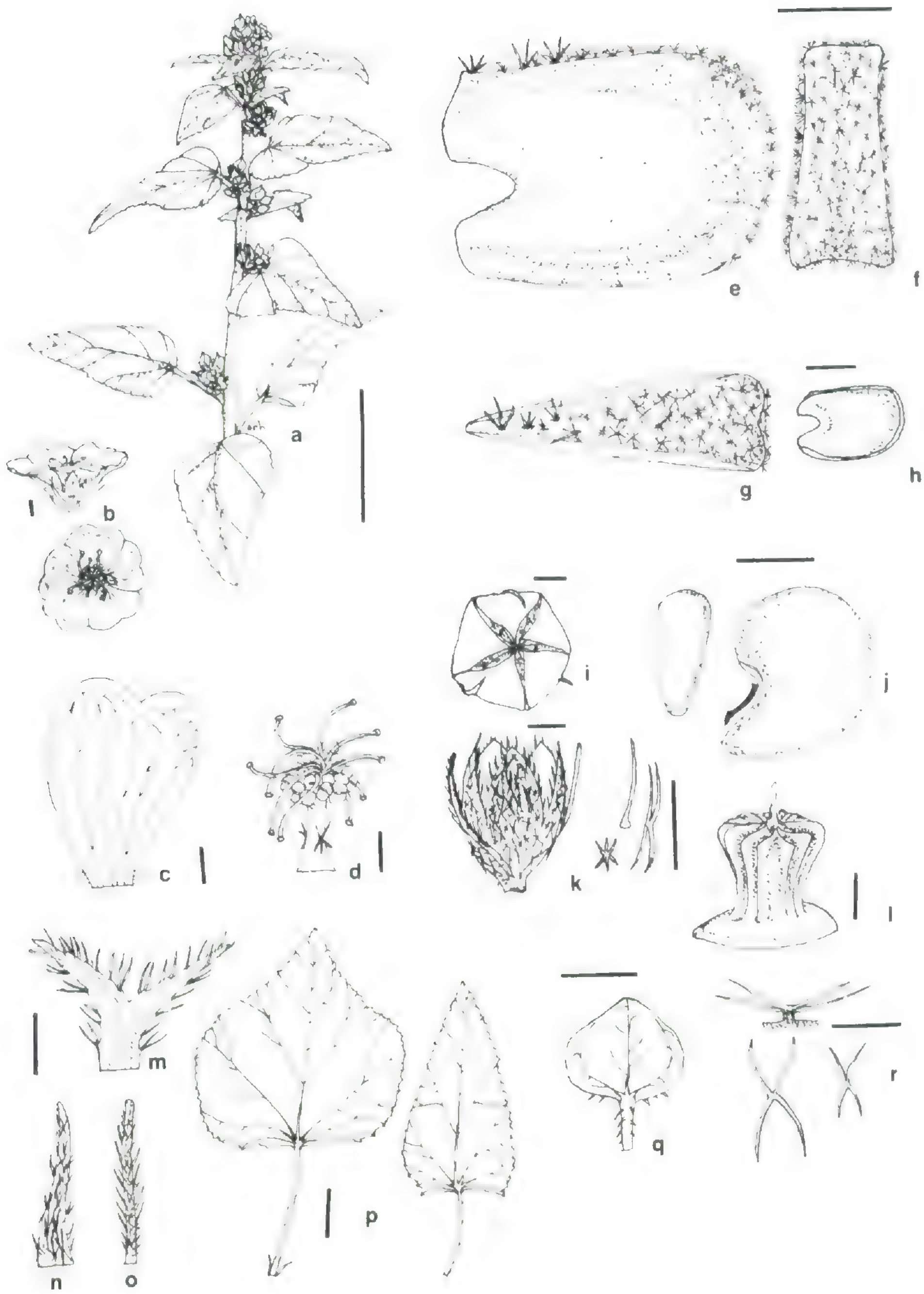


Figure 23. Distribution of *Malvastrum spiciflorum* and *M. interruptum*.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pedicels 0.5–1.5 mm long, scarcely increasing in fruit by less than 1 mm; *involucel* of 3 linear bracteoles 4–5 mm long × 0.3–0.6 mm wide completely free from the calyx or scarcely adnate in the basal 0.5 mm; *calyx* united 1/3 to 1/2 its length, 4.0–4.5 mm long increasing to 8 mm in fruit, broadly campanulate in flower and with incurved lobes in fruit, lobes triangular, acuminate-cuspidate, 5.0–6.5 mm long × 4.0 4.5 mm wide in fruit, abaxial vesture of sparse or dense 4-rayed hairs 1.5 mm diam and 4–6-rayed appressed stellate hairs 0.2–0.8 mm diam and usually with simple apically directed marginal hairs 1.0–1.5 mm long, adaxial surface of lobes puberulent on upper half and marginally with minute simple hairs; *corolla* pale yellow, petals slightly asymmetrically bilobed 7 8 mm long (5–6 mm in dried specimens) × 4–5 mm wide, broadly campanulate, exceeding the calyx by 2 3 mm, claw slightly pubescent basally and marginally with fine simple hairs; *androecium* with 20–22 (27) stamens, filament tube 1.5–2.0 (-2.5) mm long, sparsely pubescent or subglabrous with 1–5 fine-textured 5-rayed stellate hairs 0.5–0.8 mm diam, rarely glabrous, free portion of filaments 1.0 mm long; *gynoecium* with 10–12 carpels, the style branching 1.5–2.0 mm above the columella exceeding the anthers by 1.5–2.0 mm, divergent and usually recurved, each stigma expanded and hemispherical; *schizocarps* 4.5–5.0 mm diam; *mericarps* 10–12, 1.9–2.0 mm in height × 2.0–2.2 mm in length × 0.8–1.0 mm in width, slightly mucronate with a mucro 0.1 mm long or less at the proximal apex, otherwise unornamented, lateral surfaces minutely granular in appearance, unribbed or with slight marginal ribs, vesture of the apical-distal and apical-marginal portion of the lateral surfaces consisting of 2–8-rayed stellate hairs 0.1–0.3 mm diam, a few of the

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Figure 24. *Malvastrum interruptum*. a. Habit, scale = 5 cm. b. Flower, scale = 2 mm. c. Petal, scale = 2 mm. d. Stamens, styles and stigmas, scale = 1 mm. e.–g. Mericarp, lateral, distal, and apical views, scale = 1 mm. h. Mericarp, internal view, scale = 1 mm. i. Fruit, apical view (vesture not indicated), scale = 2 mm. j. Seed, apical and lateral views, scale = 1 mm. k. Calyx in flower and calyx hairs enlarged, scales = 2 mm and 1 mm respectively. l. Columella and carpocrater, scale = 0.5 mm. m. Floral bract, scale = 2 mm. n .Stipule, scale = 2 mm. o. Bracteole, scale = 2 mm. p. Leaves, basal and midstem, scale = 2 cm. q. Cotyledon, scale = 5 mm. r. Stem hairs, scale = 1 mm. (a -d, i–l, o–q from cultiv. progeny of *Gutiérrez 357*; e–h from *Bailetti 195;* m,r from *Lorentz 276;* n from *Meyer 3675*).

proximal-apical hairs with enlarged rays 0.5 mm long, lateral surfaces of pericarp over the seed translucent and chartaceous, somewhat woody and opaque on remainder, thin and fragile and usually fragmenting to release the seed, indehiscent, endoglossum lacking, mericarp tardily deciduous from the calyx due to the incurved lobes; *seeds* 1.5–1.6 mm in height × 1.5–1.6 mm in length × 0.8–0.9 mm in width; *chromosome number:* $n = 18$, $2n = 36$; *pollen* 60–82 (70) μm diam, echinae 3.9–5.1 μm, apertures 6–11.

DISTRIBUTION. (Fig. 23). Restricted to the foothills and mountainous regions from San Luis and Córdoba, Argentina in the south, north to La Paz, Bolivia, at elevations of 500 m in the south to 2700 m in the north.

PHENOLOGY AND REPRODUCTIVE BIOLOGY. Where indigenous, flowering from January to May (local summer and autumn) and occasionally as early as November, the old fruits often persist throughout the year. Some seeds are viable for at least 27 years. In greenhouse-grown plants in Texas (seeds from *Gutiérrez 357* and *Krapovickas et al. 22103*) seeds germinated in 1–3 weeks, and the plants produced their first flowers in late-August and early September (local late summer and early autumn) after 100–120 days of growth and continued flowering until December. Flowers generally opened at 3–3:30 pm CST and closed at 5:30–6 pm CST. Anthers failed to dehisce in the elevated greenhouse temperatures in August and September (29°–35° C) but dehiscence was normal in October and November. The stigmas were well-separated from the anther column but tended to recurve and thus self-pollinate by the time the flower wilted. Emasculated flowers did not set fruit. Fruits were mature 21–26 days after pollination.

DISCUSSION. During the latter half of the last century this species was often confused with *Malvastrum americanum* (then usually known as *M. spicatum*) since at full maturity the upper axillary spikes merge to form what appears to be a single terminal spike and because both species are rather robust. Actually the two species have no obvious relationship and are only superficially similar in that one regard. When its characters are examined it is seen to resemble more strongly *M. spiciflorum*. The plant is a hexaploid, without any close similarity to the only other known hexaploid in

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Figure 25. *Malvastrum interruptum* (lectotype).

Malvastrum interruptum K. Schumann
(Iso-)Syntypus

Herb. Goettingen

the genus, *M. aurantiacum*. It is my impression that this and *M. spiciflorum* are old species within the genus and have inhabited their present ranges in the stable upland Pampean massif region perhaps since their first appearance with minor changes in range during glaciation.

REPRESENTATIVE SPECIMENS: **Argentina.** CATAMARCA: Dpto. Ambato, Alrededores del Rodeo, *Cristóbal 415* (UC); CÓRDOBA: Dpto. Calamuchita, Dique los Molinos, *Krapovickas & Cristóbal 14719* (C, pf); Dpto. Colón, Ascochinga, *O'Donell & Rodrigues-V. 406* (A, U); Dpto. Punilla, Puerto Punilla, *Gutiérrez 357* (NY, SMU); La Falda, *Rodrigo 2297* (NY); Dpto. Santa Maria, Puesto el Cura, *Pierotti s.n.* (U); JUJUY: Dpto. Capital, 25 km NE of Jujuy, *Eyerdam & Beetle 22209* (GH, K, UC); Dpto. Tumbaya, Volcán, *Cabrera 12164* (F); SALTA: Dpto. Candelario, Agua Caliente, *Venturi 3728* (GH); Dpto. Chicoana, 16 km W of Chicoana, *Krapovickas et al. 22103* (pf); Dpto. Rosario de Lerma, Campo Quijano, *Meyer 3675* (GH, NY); SANTA FE: Rosario, *Schnyder s.n.* (US); TUCUMÁN: Dpto. Burruyacu, Cerro del Campo, *Bailetti 195* (A); Dpto. Capital, *Lillo 2238* (G); Dpto. Río Chico, Escoba (Cumbre de Santa Ana), *Monetti 1698* (U); Dpto. Tafí, *Venturi 801* (A, U, US); Dpto. Trancas, Río Taipamayo, *Venturi 4310* (US); **Bolivia.** COCHABAMBA: Valle del Cercado de Cochabamba, *Steinbach 185* (GH, U, UMO); LA PAZ: Illimani, *Buchtein 3214* (GH, NY, US); TARIJA: Tarija, Escuela de Agricultura, *Krapovickas et al. 18808* (pf, UC).

Section 3. *Americanum*

Malvastrum sectio **Americanum** S. R. Hill, *sect. nov.*

Carpella matura 7–18, indehiscentia vel partim basi et margine proximali-apicali dehiscentia muris lateralibus pericarpii crassis, pilis simplicibus vel pilis stellatis infrequenter cum simplicibus intermixtis, inornata vel mucrone proximali-apicali singulo minuto minore quam 0.2 mm longitudine, marginibus pericarpii angulatis, endoglosso praesenti vel nullo; stamina 18–49, columna staminali pubescenti; flores (1–5) solitarii axillares, demum in spicis vel racemis terminalibus foliaceis infra majoribus quam 3 cm longitudine; bracteolae involucelli basi ad calycem adnatae vel liberae; bracteae florales bifidae praesentes; pili caulini nunquam stipitati; pollinis grana aperturis 6–8. Typus: *Malvastrum americanum* (L.) Torrey.

The compact leafy terminal spikes or racemes, firm-walled briefly mucronate or unornamented mericarps, pubescent filament tube, bifid floral bracts, and 6–8 aperturate pollen characterize the section *Americanum*.

4a. **Malvastrum americanum** (Linnaeus) Torrey in Emory var. **americanum,** Rep. U.S. Mex. Bound. Surv. **2**, 1.Botany: 38. 1859. Fig. 26, 27.

Malva americana Linnaeus, Sp. Pl. 2: 687. 1753. TYPE: Hortus Leydensis, *A. van Royen s.n.* (LECTOTYPE: L 908.139-311 PROBABLE ISOTYPE: G!). See discussion. *Malveopsis americana* (Linnaeus) O. Kuntze, Rev. Gen. 1: 72. 1891, quoad basionym, excl. syn. et specim. Kuntze misapplied this name to *M. coromandelianum* (L.) Garcke. *Sphaeralcea americana* (Linnaeus) Metz, Catholic Univ. Amer. Biol. Ser. **16**: 142. 1934, quoad basionym, excl. specim. Metz misapplied this name to *M. coromandelianum* (L.) Garcke.

Malva spicata Linnaeus, Syst. Nat. ed. **10**, 2: 1146. 1759. TYPE: Jamaica, *H. Sloane s.n.* (LECTOTYPE: Sloane Herbarium, BM-(photo Killip neg. no. 616-F!, G!, US!)). See discussion. *Malva spicata* Linnaeus var. *β foliis-subcordatis* De Candolle, Prodromus 1: 430. 1824. Described as the typical form of Linnaeus' species. *Malvastrum spicatum* (Linnaeus) A. Gray, Mem. Amer. Acad. Arts n.s. **4**: 22, in adn. 1849. *Malveopsis spicata* (Linnaeus) O. Kuntze var. *α normalis* O. Kuntze, Rev. Gen. **1**: 72. 1891.

Malva gangetica Linnaeus, Sp. Pl. ed 2, 2: 967. 1763. TYPE: t. 74, f. 6 in Plukenet, Phytographia, 1692, apparently the sole basis for the name, is chosen as lectotype. See discussion.

Malva ovata Cavanilles, Diss. Bot. **2**: 81, t. 20, f. 2. 1786. TYPE: *Commerson s.n.* (HOLOTYPE: C!). See discussion. *Malva spicata* Linnaeus var. *α foliis-ovatis* De Candolle, Prodromus **1**: 430. 1824. Based upon Cavanilles' plate; there are no specimens in the De Candolle Herbarium (G-DC) bearing this name.

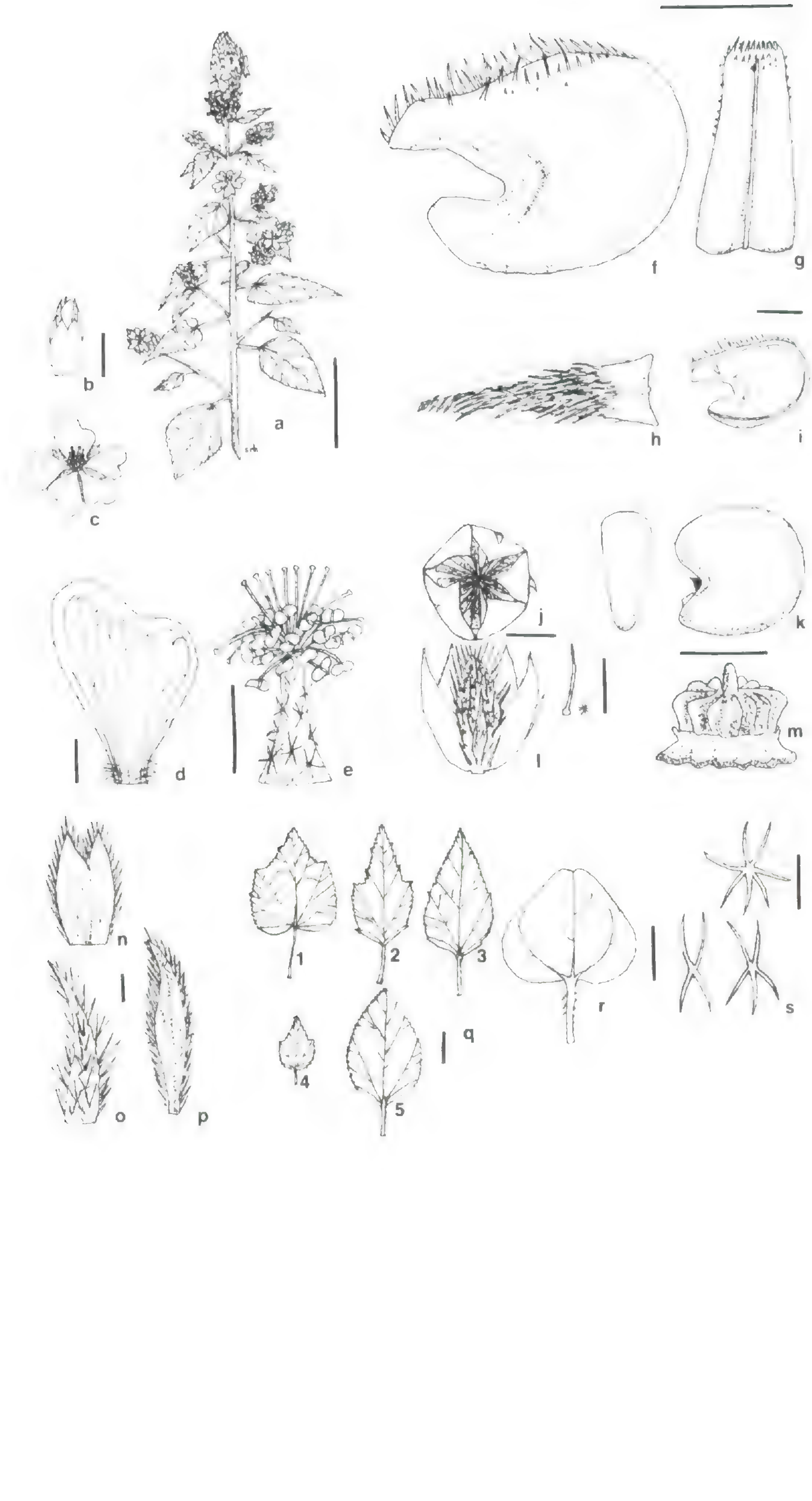
Malva polystachya Cavanilles, Diss Bot. **5**: 281, t. 138, f. 3. 1788. TYPE. *Lagasca s.n.* cultiv. in R. H. Matritensis, (LECTOTYPE: G). See discussion.

Malva curassavica Desrousseaux in Lamarck, Encycl. 3: 754. 1792. TYPE: Not determined. Desrousseaux stated that he had seen dried specimens from Curação and also cited Breynius (Exot. Pl. Cent.: 124, t. 57. 1678), the latter cited by Linnaeus as *M. americana*. Specimens should be sought at P-LA.

Malva betulina Desrousseaux in Lamarck var. *β*, Encycl. 3: 754. 1792. TYPE: plants raised from seed at Hortus Parisiensis from seed in part sent by Martín, Santo Domingo; a single leaf represents this variety, mounted with the typical variety, which is *M. corchorifolium* (HOLOTYPE: P-LA); confirmed by Krapovickas (pers. comm.).

Malva sublobata Desrousseaux in Lamarck, Encycl. 3: 754. 1792. TYPE: no authentic specimens known, but may exist at P-LA. Desrousseaux stated that he had observed this species at Hortus Parisiensis growing under the name *Malva gangetica;* his description clearly refers to *Malvastrum americanum*.

Malva borbonica Willdenow, Enum. Plant.: 728. 1809. TYPE: Mauritius and Réunion (fide descr.) (LECTOTYPE: B-W-microfiche no. 12749, sheet 2). In the Willdenow herbarium under no. *12749* are two specimens: sheet 1 bears a fragment of *Melochia corchorifolia* and of *Malvastrum coromandelianum,* and sheet 2 bears a specimen of *M. americanum;* the original description fits the latter specimen particularly well. In the Bernhardi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Herbarium (MO) there is a specimen under this name, but no additional data is given; it may or may not be an isotype.

Malva trachelifolia Link, Enum. Plant.: 209. 1822. TYPE: The description may serve as type, as Link's Berlin types have been lost. The description best fits *M. americanum,* indicating yellow flowers, cordate leaves, and a capitate inflorescence. *Malvastrum trachelifolium* (Link) Ulbrich, Feddes Repert. Spec. Nov. Regni Veg. **13**: 509. 1915.

?*Malva lagascae* Hort. ex De Candolle, Prodromus 1: 430. 1824, pro syn., nom. nud. The specimen upon which this name was based (TO - photo srh!) may be a sterile specimen of *M. americanum* and is tentatively assigned here. The specimen has briefly 3-lobed leaves, but the petioles are rather long for *M. americanum.*

Malva timoriensis De Candolle, Prodromus 1: 430. 1824. TYPE: Timor, ex Museum de Paris, 1821, ? *Riedlé s.n.* (HOLOTYPE: G-DC - microfiche 430.7; ISOTYPES: G!, K!, L 908.137-308). *Malva blumeana* Steudel, Nom. Bot. ed. 2, **2**: 94. 1841. Steudel's name was based upon *Malva timoriensis* cited in Blume (Bijdr **2**: 64. 1825) thought to be possibly different from that of De Candolle which it apparently is not.

Malva fluminensis Vellozo, Fl. Flumin.: 287. 1825. et Icones 7: t. 48. 1831. TYPE: Brazil, Rio de Janeiro, seacoast, presumably collected by Vellozo. Specimen, according to Vellozo, in the "Cabinet d'Histoire naturelle de Rio de Janeiro". (?RB) No specimens seen. Both the description and plate clearly indicate *M. americanum.*

Malva macrostachya Presl. Rel. Haenk. 2, **2**: 120. 1835. TYPE: Mexico: Guerrero. Acapulco harbor, 1790? *T. Haenke ?s.n.* (HOLOTYPE: presumably PR, not seen). The description clearly indicates *M. americanum,* known to occur in this area. *Malveopsis macrostachya* (Presl) O. Kuntze, Rev. Gen. **1**: 72. 1891.

Malva astrolasia Zippel ex Spanoghe, Linnaea **15**: 168. 1841. nomen nudum, pro syn. Listed as a synonym of *Malva timoriensis* De Candolle. No specimens cited, presumably based on a Zippel collection; a manuscript name.

Figure 26. *Malvastrum americanum* var. *americanum.* a. Habit, scale = 5 cm. b. Flower bud with bract, hairs not included, scale = 5 cm. c. Flower, scale = 5 mm. d. Petal, scale = 2 mm. e. Stamens, styles, and stigmas, scale = 2 mm. f.–h. Mericarp, lateral, distal and apical views, scale = 1 mm. i. Mericarp, internal surface, scale = 1 mm. j. Fruit, without vesture, scale = 2 mm. k. Seed, scale = 1 mm. l. Calyx in flower, vesture of one lobe indicated, and hairs, scales = 2 mm and 1 mm, respectively. m. Columella and carpocrater, scale = 1 mm. n .Floral bract, adaxial surface, scale = 1 mm. o. Stipule, abaxial surface, scale = 1 mm. p. Bracteole, adaxial surface, scale = 1 mm. q. Mid-stem leaf variation, scale = 2 cm. r. Cotyledon, scale = 2 mm. s. Stem hairs, scale = 0.5 mm. (a–b, q(5) from progeny of *Silva-Santos 28017;* c d, f–j, m from *Hill 8093;* e, o–p from *Hill 6054;* k–l from *Croat 21340;* n,q(2),s from *Ventura 2622;* q(1) from *Dorantes, et al. 5369*; q(3) from *Romero-Castañeda 10570;* q(4) from *Board 1098;* r from progeny of *Koch & Fryxell 78290*).

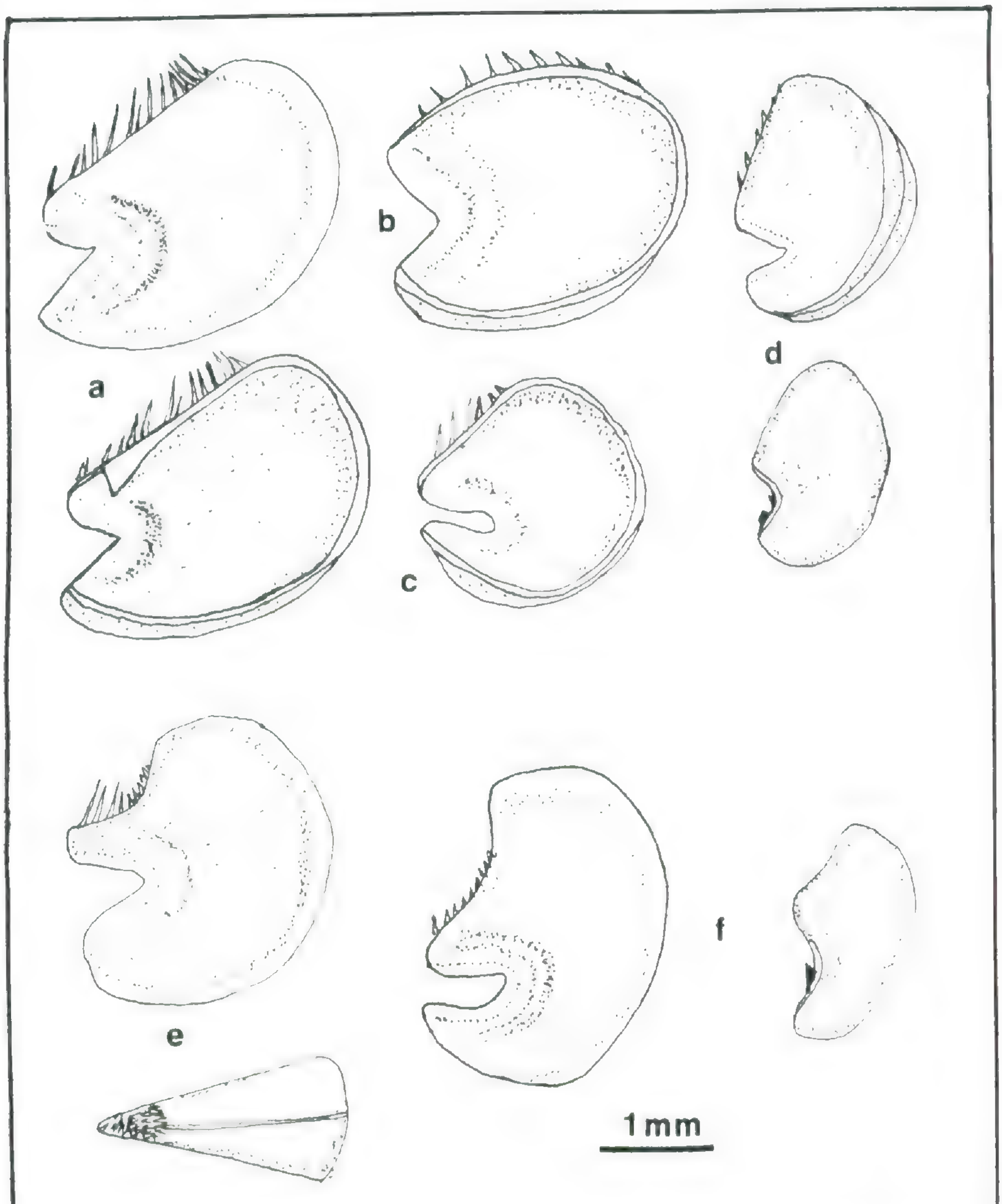


Figure 27. Mericarp and seed variation in *Malvastrum americanum* var. *americanum* in Australia. a. *Purdie & Boyland 35*, lateral and internal views. b. *Adams 1058*. c. *Sillar 2*. d. *Hubbard 7382*, external view and seed (lower). e. *Blake 8894*, external and apical views, f. *Michael 1287*, lateral view and seed.

Malva brachystachya F. von Müller, Linnaea **25**: 378. 1853. TYPE: Australia, rocky and shaded margins of Sulteyer Creek and Mt. Gullert Creek, Flinders Range, *F. von Mueller s.n.* (SYNTYPES: BM, K, MEL). Müller mistakenly referred to "*M. ovata* Hook. in Mitchell trop. Austr. 397, non Cavanilles" as the basis of the name thinking it a later homonym. Hooker was explicitly referring to Cavanilles' plant. Müller's name is based on a separate type.

Malveopsis spicata (L.) O. Kuntze var. *α normalis* O. Kuntze f. *flava* O. Kuntze, Rev. Gen. 1: 72. 1891. Kuntze's entire description and citation consists of the following: "Flores flavi. Portorico." No Kuntze specimens from Puerto Rico have been seen, and it seems as if the name was based upon an assemblage of typical specimens from that island.

Malveopsis spicata (L.) O. Kuntze var. *α normalis* O. Kuntze f. *rubra* O. Kuntze, Rev. Gen. 1: 72. 1891. "Flores rubescentes. Trinidad." No Kuntze specimens from Trinidad have been found. Kuntze probably based this name on dried specimens whose corolla had faded to a pink tint, not infrequently seen.

Malveopsis spicata (L.) O. Kuntze var. *β pauciflora* O. Kuntze, Rev. Gen. 1: 72. 1891. "Flores axillares solitarii". No specimens were cited. Probably based upon young specimens of *M. americanum*.

Malveopsis spicata (L.) O. Kuntze var. *β pauciflora* O. Kuntze f. *flava* O. Kuntze, Rev. Gen. 1: 72. 1891, nomen nudum. Said to be from Trinidad, Kuntze likely considered this to be the typical form of his variety, but did not explicitly say so and supplied no description.

Malveopsis spicata (L.) O. Kuntze var. *β pauciflora* O. Kuntze f. *aurantiaca* O. Kuntze, Rev. Gen. 1: 72. 1891, nomen nudum. Presumed to be from Venezuela: Porto Cabello. The listing is not clear. No description is given for this form, and it seems to be associated with the next variety in this listing.

Malveopsis spicata (L.) O. Kuntze var. *ovata* O. Kuntze, Rev. Gen. 1: 72. 1891. This name is attributed to Grisebach without a citation, but Grisebach is not known to have published this name. The description and citation follows: "Folia minora haud lobulata. Venezuela: Porto Cabello." No Kuntze specimens from this area have been found. The name does not seem to be based on that of Cavanilles. The name was probably based upon xerophytic forms or old individuals of the species.

Malvastrum spicatum (Linnaeus) A. Gray var. *mollissima* Chevalier, Rev. Bot. Appl. Agr. Trop. 15: 944. 1935. TYPE: Cape Verde Islands: Boa Vista, near Sal Rei, 1934, *A.J.B. Chevalier 44,367* (LECTOTYPE: P). Based upon dwarfed, apparently grazed forms of the species.

Herbaceous to suffrutescent often bushy-branched perennial (0.4) 1.0–2.0 (3) m tall; *main stem* (3) 4–10 (15) mm diam at the base, *primary branches* (10) 30–100 cm long, stem canescent with overlapping sessile or infrequently pustular-based (5) 6–8 (10)-rayed stellate hairs (0.3) 0.8–1.5 mm diam tardily shed in age; *cotyledons* ca. 7 mm long × 8 mm wide, wide-ovate, apex emarginate, base

subcordate to subtruncate; *stipules* (2) 3–5 (8) mm long × 0.6–1.0 mm wide, subfalcate, lanceolate, acuminate; *petioles* (15) 35–80 (100) mm long on early vegetative or lower stem leaves, considerably reduced to (4) 10 15 (30) mm on leaves near branch apices and on xerophytes; *blades* (1.2) 1.5–2.2× longer than petioles in lower leaves and (2.1) 3 5 × longer in apical leaves, early vegetative and midstem leaves (40) 50 115 (145) mm long × (25) 40 100 (140) mm wide and those towards branch apices and inflorescences or on xerophytes (11) 20–40 (50) mm long × (7) 15–30 (40) mm wide, average midstem blade 1.2 1.6 × longer than wide, ovate wide-ovate to ovate-lanceolate, often briefly 3-lobed ca. halfway from the cordate truncate to rounded or wide-cuneate base, apex acute to acuminate, margin dentate in lower leaves to denticulate in upper leaves with 2–7 teeth/cm, vesture of the adaxial surface of regularly arranged scarcely to slightly overlapping (5) 6 (8)-rayed stellate hairs 0.8–1.2 mm in diam, abaxial surface pubescent with similar scattered (8) 10 12-rayed stellate hairs usually 0.3–0.8 mm diam; *flowers* (the first 1–2) infrequently solitary axillary, then in congested terminal spikes (2) 3 10 (18) cm long × 12 17 mm diam terminating every branch, flowers subtended by a bifid *floral bract* divided 1/3 to 1/2 its length, (3) 4–5 (6) mm long × 2 mm wide; *pedicels* essentially lacking, up to 3 mm long on the early solitary flowers and 0.1 mm on flowers in spikes, not lengthening in fruit; *involucel* of 3 lanceolate, subfalcate, acute to acuminate bracteoles (4) 5–7 (9) mm long × 0.8–1.5 mm wide, equalling or exceeding calyx-lobes by < 1 mm in flower, adnate to the calyx in the basal (1.0) 1.5–2.0 mm; *calyx* united 1/4 to 1/3 its length, broadly campanulate in flower, indistinctly angled, 5 6 mm long increasing to 6–10 mm in fruit, the triangular to deltate lobes generally incurved and slightly accrescent in fruit, 3 mm long × 2–2.5 mm wide in flower and 5–7 mm long × 4 mm wide in fruit, abaxial surface rather densely hirsute with scattered appressed rigid apically directed simple hairs 1.0 1.5 (2.0) mm long mixed with minute 5 8-rayed closely appressed stellate hairs 0.05 0.3 mm diam and with a few stellate hairs similar to those of the stem, adaxial surface subglabrous with a few minute arachnoid hairs on the apical and medial 1/3 continuing marginally to the sinus; *corolla* (12) 13–15 (17) mm diam at anthesis, orange-yellow, petals obovate and briefly asymmetrically lobed, 6 8 (10) mm long × 4 5 (6) mm wide, rotate and nearly planar, exceeding the calyx by 2 3 mm, claws ciliate with

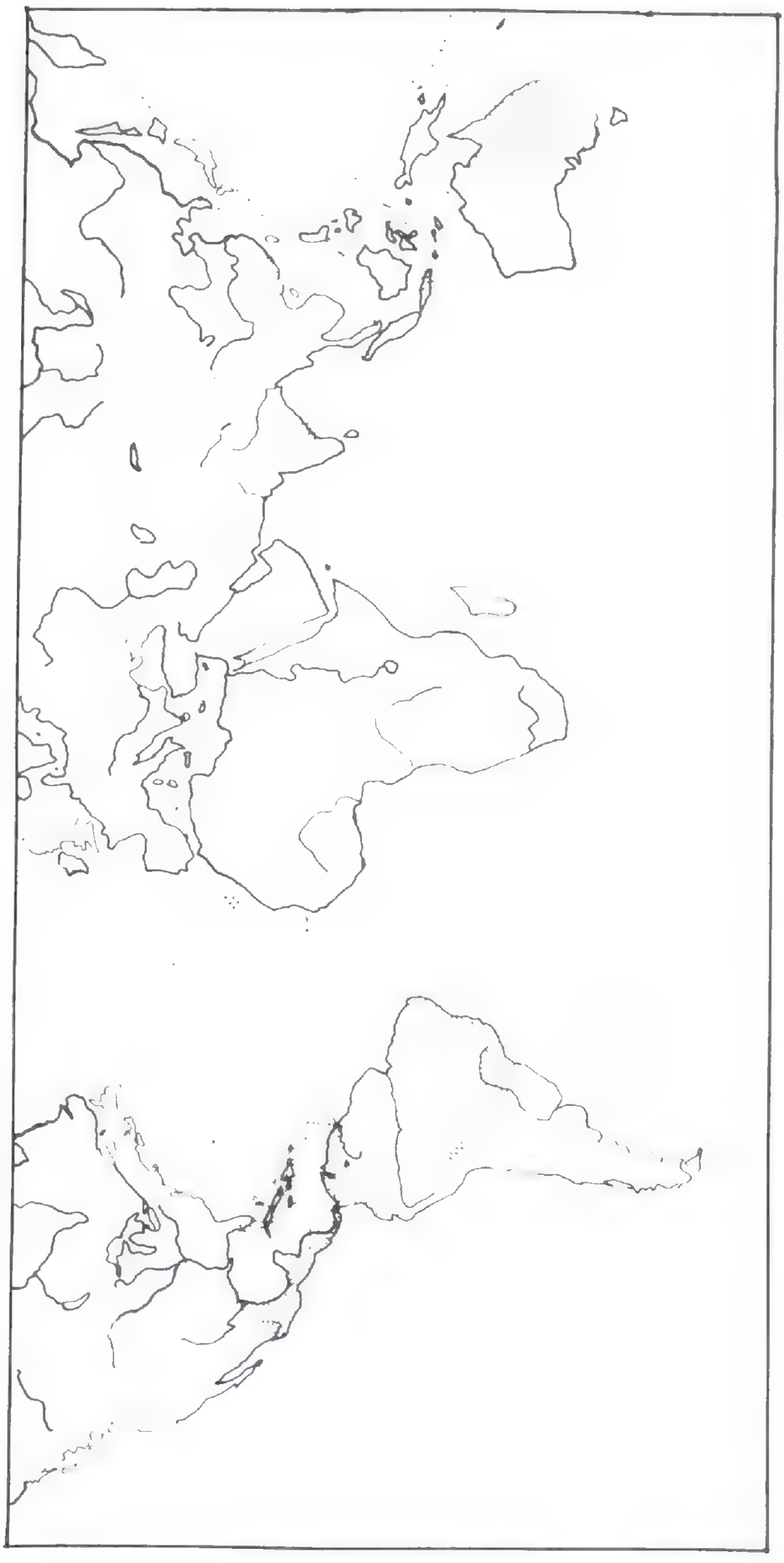


Figure 28. Distribution of *Malvastrum americanum* var. *americanum*.

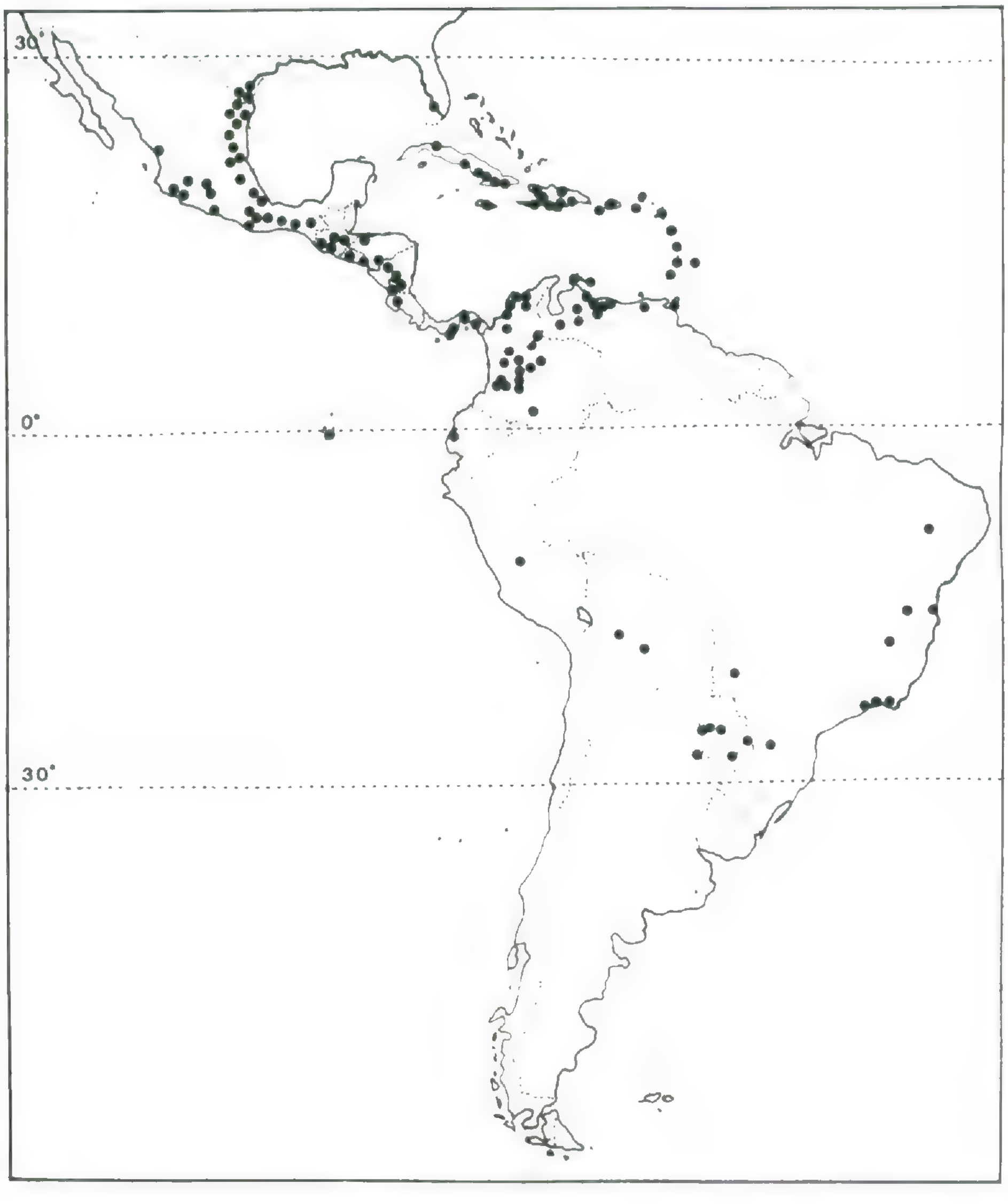


Figure 29. Western Hemisphere distribution of *Malvastrum americanum* var. *americanum*.

tufted simple or stellate hairs 0.5 0.8 mm long; *androecium* of (18) 30-40 (49) stamens, filament tube 2.0–2.5 (3.0) mm long, pubescent with delicate 2–6-rayed stellate hairs 0.2–0.5 mm diam, free portion of filaments 1.0 mm long, anthers 0.5 0.7 mm long × 0.3–0.4 mm wide after dehiscence; *gynoecium* with (9) 10–15 (18) carpels, the style branching 2.5–3.0 mm above the columella, each branch terminated by a slightly expanded subglobose papillose stigma

exserted 1.0–1.5 mm beyond the anther cluster, reflexed at flower wilt; *schizocarps* (4.0) 5–6.0 mm diam; *mericarps* (9) 10–15 (18), conspicuously separate from one another, 1.5–2.0 mm in height × 1.5–2.5 (3.0) mm in length × 0.8 mm wide rarely vertically elongated, usually with a minute proximal-apical mucro <0.1 mm long, lateral faces conspicuously or inconspicuously ribbed, distal-basal surface with a somewhat inconspicuous raised medial line, vesture of ascending simple rigid hairs 0.1–0.5 mm long directed proximally and restricted to the apical surface and the extreme apical margin of the lateral surfaces, pericarp chartaceous over the seed, firm distally, often partially dehiscent along the basal-proximal midline and releasing the seed while still in the calyx, and weakly dehiscent at the proximal-apical margin but the valves not separating, endoglossum 0.3 mm long positioned 0.3 mm distal to the proximal margin (except in some Australian populations in which it is reduced or absent), mericarps and seeds tardily shed from the calyx due to the lobe orientation; *seeds* 1.3–1.5 mm in height × 1.3–1.7 mm in length × 0.6–0.8 mm wide; *chromosome number:* $n = 12$, $2n = 24$; *pollen* (41) 51.2–72 (60) μm diam, echinae 3–5 μm, apertures 6–10.

DISTRIBUTION. (Fig. 28, 29). Pantropical, often weedy, found in both native and introduced populations between 28° N and 28° S, most frequently in subhumid or humid regions; in the Western Hemisphere occurring from south Texas and south Florida south through the Caribbean and Central America to coastal and highland regions surrounding the Amazon basin to northern Argentina, at elevations of near sea level to 1500 m or to 2150 m near the equator. In Australia it is widespread in the eastern portion of the continent.

PHENOLOGY AND REPRODUCTIVE BIOLOGY. At the northern extreme of its range in southern Texas, *Malvastrum americanum* flowers nearly all year when sufficiently warm, from February until November. In other portions of its range it flowers at any time of the year after sufficient rainfall. Seeds up to 15 years old planted in a greenhouse at College Station, Texas (progeny of *Hill 6054, Percival s.n., Ventura 2622, Breedlove 35899, Molina 11644* and *27315, Seymour 2362, Williams et al. 23805, Fryxell 2861, Croat 21340, Trujillo 8683,* and *Silva-Santos 28017*) germinated in 4 to 14 days. The Texas plants first flowered 90 days after germination (in

late summer). Plants from the other populations did not begin flowering until mid-November after 240 days of growth, possibly due to genetic controls on maturation as well as on photoperiodicity. Plants transplanted from Texas populations (*Hill 7640*) flowered nearly all year after the transplantation.

The flowers on all populations opened at approximately 4:30–4:45 pm CST and closed at 6:30–6:45 pm CST, local sunset. This period shifted one hour later in the summer (taking into account local standard time) probably due to the increased daylight, but the duration remained the same. At the time of opening the stigmas were conspicuously remote from the anther cluster, but after one hour began to recurve and were covered with pollen at the time of flower wilt. A considerable number of pollinators were observed in the field (see Table 2). Both cross-pollination and selfing appear to be frequent in the species. Fruits were mature in 15–19 days after pollination. Emasculated flowers did not set fruit.

DISCUSSION. Problems of typification are widespread in the literature on *Malvastrum americanum*. The lectotype of *Malva americana* Linnaeus was chosen by van Borssum-Waalkes (1966, p. 154–155). Linnaeus cited van Royen (Fl. Leyd, Prod.: 357, erroneously 359. 1740) and Breynius (Exot. Pl. Cent.: 124, t. 57. 1678). Both citations clearly refer to this species. The lectotype is a specimen in the Rijksherbarium at Leiden bearing a label with van Royen's script upon which is inscribed Linnaeus' binomial as well as a reference to van Royen's own description. The specimen is considered to be part of the protologue of *Malva americana*, and its choice as lectotype seems appropriate. There are no specimens in the Linnaean Herbarium bearing this name. A duplicate specimen with all of the above script is also in Geneva, and is apparently an isotype.

Malva spicata Linnaeus was based upon a description and plate of Sloane (Voy. Jam.: t. 138, f. 1. 1707). The description in Sloane's work, p. 218, can fit *Malvastrum americanum*, but can also describe *Melochia villosa*, which t. 138, f. 1 seems to illustrate. No mention is made of flower color by Sloane. However, in the Sloane Herbarium (BM) is a specimen of *Malvastrum americanum* annotated as "Althaea spicata", here considered part of the protologue and chosen as lectotype. In the Linnaean Herbarium (LINN) is a specimen annotated as *Malva spicata* from Jamaica, under the

number 870.1. This specimen, possibly collected by P. Browne, may have been the basis for the more complete description of the species published by Linnaeus and his student G. Elmgren in a dissertation in November of the same year (Pug. Jamaic. Plant.: no. 62. 1759). There is no evidence that this specimen was seen by Linnaeus before the original description. It is unfortunate that Linnaeus was unaware that he had described the same species under a different name at an earlier date.

Malva gangetica Linnaeus was described as "Malva foliis cordatis obtusis scabris, floribus sessilibus glomeratis axillis denis muticis crenulatis" by Linnaeus (Sp. Pl. ed. 2, 2: 967. 1763), and Plukenet's illustration (Phytographia: t. 74, f. 6. 1692) was cited. This figure, while poor seems to represent a young plant of *Malvastrum americanum*. Early specimens in the Willdenow Herbarium (B-W) bearing this name (cat. no. *12750*) seem also to be immature individuals of *M. americanum*. Similar specimens occur in the Torino Herbarium (TO - no. *632*, photo srh!).

In describing *Malva ovata*, Cavanilles cited plants observed by Commerson, and specimens of Thouin. There are no specimens of the plant in the Thouin Herbarium (SBT), but a Thouin herbarium specimen bearing this name and a reference to the original publication was found at Copenhagen (C). This specimen is here chosen as lectotype. In the Cavanilles' Herbarium (MA) is a sheet with two specimens, one of which is a young specimen of *Malvastrum americanum* said to be from Brazil. The other specimen, not a *Malvastrum,* is from the Cape of Good Hope, not a locality cited by Cavanilles. Also in the Cavanilles Herbarium are two specimens labeled *Malva polystachya*. These are ineligible to be considered as lectotypes under this name as they are dated 1828, 40 years after the original description. Cavanilles' illustration agrees closely with a Lagasca specimen at Geneva grown at the Madrid Botanic Gardens and was likely based on this material.

The earlier botanists generally did not provide enough descriptive information to distinguish *Malvastrum americanum* from *M. corchorifolium*. To compound the nomenclatural problem, *Malva americana* Linnaeus was, beginning with Cavanilles (1786), often misapplied to *Malvastrum coromandelianum*. Since several of the early type specimens have not been found, some doubt concerning application must be attached to certain names in *Malva* published

before 1849. I have listed the synonyms known or suspected by me to belong in *M. americanum* above. This species is one of the few with a cordate leaf base and dense vesture and so it can often be separated from *M. corchorifolium* in early descriptions by these characters. Specimens of the two species can be readily distinguished from one another by both the distinctive vesture characters and the morphology of the reproductive parts at maturity.

In an earlier section I have put forth the hypothesis that *Malvastrum americanum* is indigenous to Australia where mericarp-number and variation as well as stamen-number do not always fit within the variation found in American populations. In many Australian specimens, the endoglossum, so conspicuous in the mericarps of American plants, is absent or highly reduced. One group of specimens have unusually elongated mericarps as well (Fig. 27) and, if it were not for a complete series of transitional forms, these could be considered a distinct variety. The extreme forms are found in a zone of selenium-contaminated soils (according to label data) and resemble, to an extent, the mericarps of *M. chillagoense*.

REPRESENTATIVE SPECIMENS: **United States.** FLORIDA: Lee Co., eastern Sanibel Island, *Brumbach 7026* (FLAS, NY); TEXAS: Cameron Co., Laguna Atacosa Nat'l. Wildlife Refuge, *Board 1098* (pf); Southmost, Brownsville, *Hill 6054* (GH, MO, NY, pf, SMU, srh); Hidalgo Co., S of Donna, *Cameron 107* (F, TEX); Kleberg Co., Laguna Larga, *Johnston 53175.28* (TEX); Nueces Co., Flour Bluff, Oso Bay, *Hill 8093* (BRI, CTES, F, GH, MO, NY, pf, SMU, srh, TAES, TEX, US, VT, WIS); Willacy Co., Sauz Ranch near headquarters, *Johnston 53175.31* (TAES, TEX).

Mexico. CHIAPAS: Mun. Tuxtla Gutiérrez, *Breedlove 19992* (DS, MICH, pf); COLIMA: Manzanillo, *Palmer 1040* (CAS, G, GH, NY, US); GUERRERO: Distr. Coyuca, Pungarabato, *Hinton et al. 7285* (F, K); JALISCO: Río San Pedro, *Gentry et al. 19553* (TEX, US); MÉXICO: Temascaltepec and Pericones, *Hinton 2958* (G, GH, K, NY, US); MICHOACAN: Tacupa, Huetamo, *Hinton 5623* (K, US); NUEVO LEON: Monterrey, *Pringle 1938* (CAS, F, G, GH, K, MICH, NY, PH, RSA, UC, US, VT); OAXACA: N of Jayacatlan along road to Nacaltepec, *Breedlove 35899* (CAS, pf, TEX); 25 km N of Juchitan, *Koch et al. 78290* (pf); SAN LUIS POTOŚI: 2–3 mi W of El Naranjo, *King 3981* (F, NY, TEX, UC, US); SINALOA: Mazatlán, *Ortega 736* (GH, K, POM); TAMAULIPAS: El Rosario near Marmolejo, *Bartlett 10865* (DS, GH, MICH, TEX, US); VERACRUZ: Laguna de la Mancha, Actopan, *Dorantes et al. 5369* (pf); S of Tampico between K 125 130, *Percival s.n.* (pf); Cerro Gordo near Salto del Río Grande, *Ventura 2622* (DS, F, MICH, NY, pf, TEX).

Guatemala. CHIQUIMULA: between Chiquimula and Santa Rosalía, *Molina & Molina 25145* (NY); ESCUINTLA: near San José, *Standley 64203* (F, NY); GUATEMALA: Sanarate, *Kellerman 6670* (F, US); JUTIAPA: Jutiapa, *Standley 75723* (F, G); RETALHULEU: Champerico, *Standley 66645* (F); SANTA ROSA: near Cuilapa, *Standley*

78535 (F); ZACAPA: Zacapa, *Standley 74380* (F); **El Salvador.** AHUACHAPÁN: near Achuapán, *Standley 20027* (GH, NY, US); SAN MIGUEL: Laguna Lomega, *Standley 21005* (GH, US); **Honduras.** SWAN ISLANDS: *Nelson 100* (GH); COPÁN: near Quebracho, *Molina 24657* (NY); CORTES: Río Chamelecon, *Molina 11644* (F, NY, US); EL PARÁISO: between El Paraíso and Villa Humada, *Molina 27201* (F, MICH, US). **Nicaragua.** BOACO: Potrerillas, Rte. 7, *Seymour 2362* (F, GH, MO, SMU, UC): CHONTALES: 5 km SE of Juigalpa, Rte. 7, *Hamblett 1614* (GH, MO, NY, SMU, UC, WIS); ESTELÍ: 3 km from Condega, *Molina 23201* (DS, NY); LEÓN: Nagarote, *Seymour 2385* (GH, MO, SMU); MANAGUA: east shore of Lago de Managua, N of Tipitapa, *Fryxell 2861* (pf); MATAGALPA: 5–10 m W of Matagalpa, *Williams et al. 23805* (F, G, TEX); NUEVA SEGOVIA (Madriz): Finca El Chile, 10 km from Somoto, Hwy. to border, *Molina 27315* (F, MICH); RIVAS: La Virgen, Rte. 16 at K 136, *Zelaya 1242* (GH, MO, NY, SMU, UC, WIS). **Costa Rica.** GUANCASTE: La Cruz, *Pittier 2744* (US). **Panama.** COCLE: 10 mi E of Nata, Río Grande, *Tyson 5249* (MO); DARIEN: vicinity of Yape, Río Tuira, *Allen 4299* (G, GH, NY); HERRERA: banks of Río Santa Maria, *Burch et al. 1189* (GH, K, MO, NY, UC, US); LOS SANTOS: 5 mi S of Pocri, *Croat 9740* (MO); PANAMA: Panama, *Porterfield s.n.* (NY); CANAL ZONE: near Playa Venado, *Wilbur & Teeri 12972* (DS, GH, MICH, NY, TEX).

Cuba. HABANA: Havana, *Boldo s.n.* (F); LAS VILLAS: Santa Clara, Ranchuelo, *Cuesta 605* (NY); MATANZAS: valley of the Canimar, *Britton et al. 365* (NY); ORIENTE: Guantanamo Bay, *Britton 1916* (F, NY, US). **Haiti.** GONAVE ISLAND: Anse Galette, *Leonard 3113* (US); TORTUE ISLAND: tableland west of La Vallée, *Leonard & Leonard 11260* (BH, BKL, US); NORD-OUEST: Bassin Bleu, *Leonard & Leonard 14787* (US); NORD: Mt. La Mine, *Leonard 7347* (GH, US); ARTIBONITE: Gros Morne, *Leonard 9978* (US); OUEST: S of Port-au-Prince, *Leonard 5265* (NY, US); SUD: Miragoane, *Eyerdam 461* (GH, US). **Dominican Republic.** AZUA: valley of Neiba, Guaragua, *Howard & Howard 8358* (GH); BANÍ: La Tabla, *Liogier 17551* (NY, US); BARAHONA: *Fuertes 264* (G, GH, NY, US); BENEFACTOR: San Juan, San Juan Santiago, *Howard & Howard 9286* (GH); PUERTO PLATA: Puerto Plata, Lojas, *Jiménez 2506* (US); SAN CRISTÓBAL (Trujillo): Najayo, near San Cristóbal, *Augusto 447* (NY); SANTIAGO: Santiago, Valle del Cibao, *Ekman 16141* (B, F, US); SANTO DOMINGO: Haina, *Faris 134* (US). **Puerto Rico.** GUAYAMA: Aguirre (Salmar), *Goll 558* (US); MAYAGUEZ: Guayanilla, *Britton & Shafer 1855* (F, NY, US); PONCE: Coamo Springs, *Britton et al. 6342* (G, NY); SAN JUAN: Distr. Bayamón, Bayamón, *Sintenis 1080* (G, MO, NY, UC, US); CULEBRA ISLAND: *Britton & Wheeler 213* (F, NY, US); MONA ISLAND: Sardineira, *Britton et al. 1659* (NY, US); VIEQUES ISLAND: Isabel Segunda, *Shafer 2445* (CAS, NY, US). **Virgin Islands.** ST. CROIX: Mary's Fancy, *Britton 203* (NY); ST. THOMAS: *Eggert 282* (GH, NY, US); TORTOLA: Elizabeth Beach, *D'Arcy 412* (C, GH); VIRGIN GORDA: *Fishlock 59* (NY). **Jamaica.** CORNWALL: Westmoreland Parish, Bluefields, *Britton 1605* (NY); MIDDLESEX: Manchester Parish, Mandeville, *Norman 78* (MO); SURREY: Kingston Parish, Kingston, *Britton & Hollick 1745* (NY). **St. Martin.** *Boldingh 2346* (NY). **St. Berthélemy.** Gustavia, *Questel 10* (NY). **St. Eustatius.** Orangestad, *Shiffers 3864* (GH). **Antigua.** Parry's Hill, *Box 917* (F, GH, MICH, MO, pf, US). **Guadeloupe.** DÉSIRADE: *Duss 3211* (F, GH, MO, NY, US); GUADELOUPE: Hautence de Bouillante, *Stehlé 105* (NY); MARIE-GALANTE: *Stehlé 476* (NY). **Martinique.** Marin to Vauchi, *Duss 858* (NY). **St. Lucia.** Cap Estate, *Sturrock 336* (GH). **St. Vincent.** *Smith & Smith 1597* (NY). **Grenadines.** GRENADA: *Bailey 427* (BH); UNION ISLAND: Chatham Bay area, *Howard*

11017 (NY). **Barbados.** St. George, *Botanic Station Herbarium 344* (F, NY, US). **Tobago.** between Scarboro & Friendship, *Druce s.n.* (OXF). **Trinidad.** CHACACHACARE ISLAND: *Cowan 1113* (US); GASPAREE ISLAND: *Britton 472* (GH, NY, US); MONOS ISLAND: *Graf 13* (NY); TRINIDAD: St. Joseph Road near the Quarry, *Broadway 7054* (G, MO, PH). **Curação.** near Williamstadt, *Britton & Shafer 2959* (NY, US). **Aruba.** *Boldingh 7012* (NY).

Venezuela. ANZOATEGUI: Guanta, *Cardona 576a* (US); ARAGUA: Maracay, *Croat 21340* (MO, pf, US); CARABOBO: between Puerto Cabello and Las Trincheras, *Alston 5725* (BM, NY, U); DISTRITO FEDERAL: Cabo Blanco, 4 mi. W of La Guaira, *Pittier 10233* (BH, GH, NY, US); FALCÓN: Adícora de Paraguaná, *Tamayo 1079* (US); LARA: near Barquisimeto, *Alston 6381* (BM); MÉRIDA: between Mérida and La Azulita, Bascopé 23 (GH); MIRANDA: near Sta. Lucía, Hacienda El Volcán, *Pittier 8280* (BH, DS, F, GH, MO, POM, UC, US); PORTUGUESA: Píritu, *Trujillo 8683* (F); TACHIRA: Cristóbal Colón, *Broadway 161* (GH, NY, US). **Colombia.** ANTIOQUIA: Dabeiba, *Barkley & Gutiérrez 1807* (NY); ATLÁNTICO: Puerto Columbia, Miramar, *Dugand 4010* (US); BOLIVAR: Cartagena, *Heriberto 218* (NY, US); BOYACÁ: Soatá, *Cuatrecasas 1032* (F, US); CUNDINAMARCA: Girandot, *Rusby & Pennell 157* (F, GH, MO, NY, US); HUILA: Río Ambicá, *Fosberg 19336* (NY, US); MAGDALENA: Santa Marta, *Smith 483* (BR, DAO, F, G, MICH, MO, NCU, NY, PH, RSA, TEX, U, US, VT, WIS); NARIÑO: road to Puerto Delicias, above Río Pureto, *Ewan 15956* (CAS, US); NORTE DE SANTANDER: La Esmeralda, *Killip & Smith 20944* (GH, NY, US); SANTANDER: Bucaramanga, *Araque & Barkley 258* (NY, UC); VALLE DEL CAUCA: 9.1 km below Dagua, *Hutchinson & Wright 3284* (MICH, MO, NY, UC, US). **Ecuador.** MANABI: Bahía de Caraquez, *Anthony & Tate 106* (US); **Galápagos.** SAN CRISTÓBAL ISLAND (CHATHAM): western coast, *Schimpff 168* (BKL, CAS, G, MO, NY, U); Wreck Bay, *Stewart 2011* (CAS); SANTA CRUZ: trail from Academy Bay to Bella Vista, *Wiggins 18471* (BH, DS). **Peru.** JUNÍN: Chacapoyas, Mathews *s.n.* (G, GH, OXF). **Bolivia.** COCHABAMBA: Tunari, *Kuntze s.n.* (NY); SANTA CRUZ: Angostura, *Steinbach 340* (F, GH, MICH, NY, U, UC, US). **Brazil.** BAHIA: Ilheus, *Herb. Martius 1010* (F, G, GH, K, MO, NY, OXF, U, US); CEARÁ: between Río Berbeiro and Crato, *Castellanos 33403* (K, NY); GUANABARA: Río de Janeiro, *Banks & Solander 1768* (MO); MATO GROSSO: Mun. Miranda, near Río Miranda, Hwy. 262, *Hatschbach 29469* (UC, US); MINAS GERAIS: Bon Cavatí, BR-4, *Silva-Santos 28017* (K, MO, NY); PARANÁ: Mun. Guaira, Porto Novo, *Hatschbach 8074* (US); RÍO DE JANEIRO: Araruama, *Sucre 774* (UB, US); SÃO PAULO: Campinas, Fazenda Sete Quedas, *Ganzaroli 6249* (CAS, UC). **Argentina:** CHACO: Casa Lata, along the Río Paraguay, *Rojas 11766* (BR); CORRIENTES: Tacombi, *Hicken 324* (NY); FORMOSA: Guaycole, *Jorgensen 3165* (GH, MO, U, US); MISIONES: Posadas, near the Alto Parana River, *Ekman 132* (MO, NY). **Paraguay.** Sapucai, *Hassler 11838* (C, F, G, GH, K, MO, NY, US). **Cape Verde Islands.** SANTIAGO ISLAND: Porto Praia, *Wright s.n.* (US); SÃO NICOLÃO ISLAND: Coelho, *Barbosa 7218* (MO).

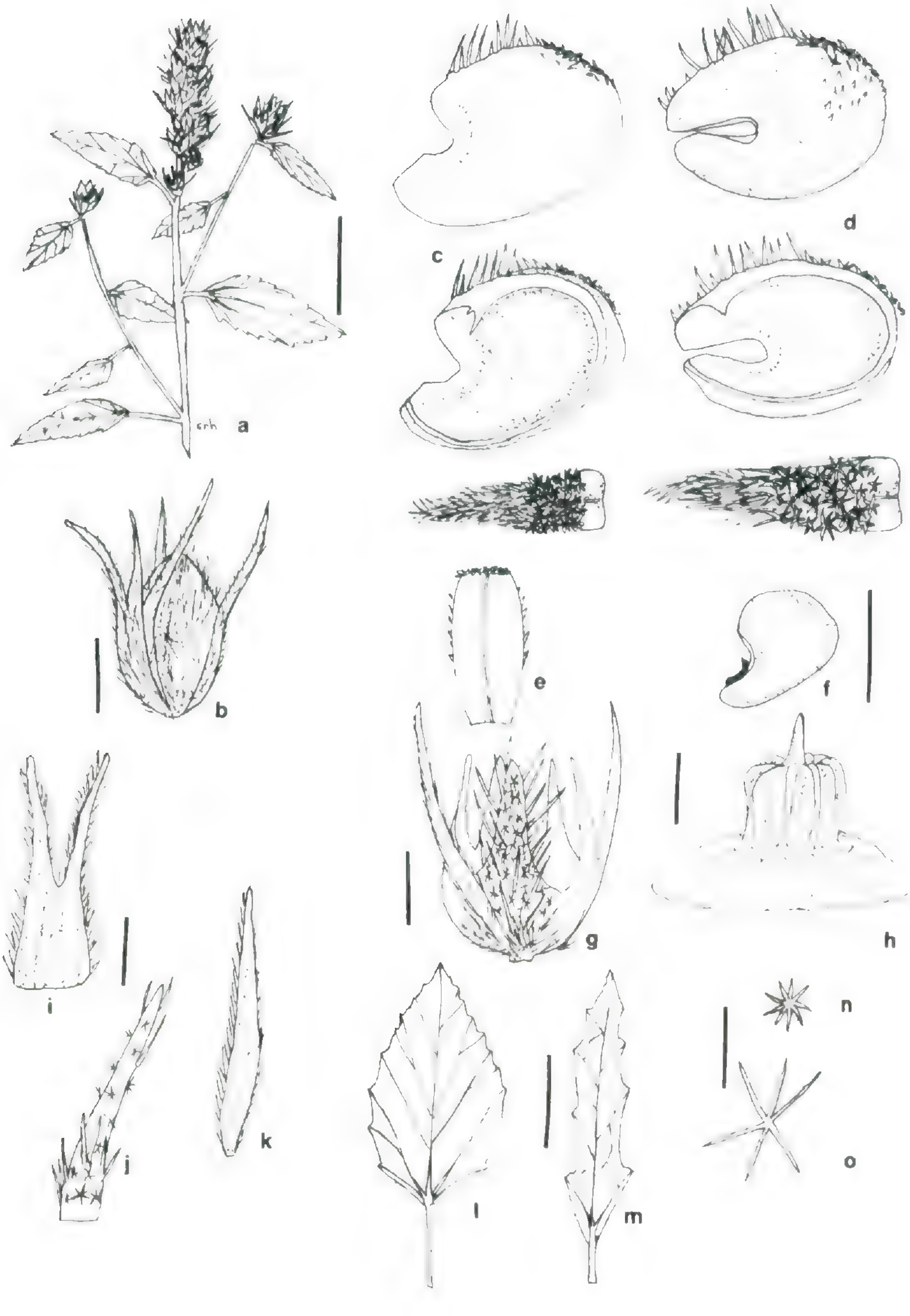
China: FUKIEN: *Chung 6530a* (NY). **Australia.** NEW SOUTH WALES: Nyngan, *Maiden s.n.* (F, G, GH, POM); NORTHERN TERRITORY: 11 mi NW of Alexandria, *Chippendale 7143* (BRI, K); NORTHWEST AUSTRALIA: Ashburton River, *von Mueller s.n.* (CAS); QUEENSLAND: S. Kennedy Distr., 3.5 mi ENE of Avon Downs station, *Adams 1058* (BRI); Gregory North Distr., Cloncurry, *Blake 8894* (BRI); Burke Distr., between Richmond and Maxwelton, *Everist 3006* (BRI, NY, US); Gregory North Distr., Duchess, *Hubbard 7382* (BRI); Charters Towers, *Michael 1287* (BRI); 10 km SE of

Charleville, *Purdie & Boyland 35* (BRI); Burke Distr., Granada, *Sillar 2* (BRI); SOUTH AUSTRALIA: Mt. Lyndhurst, *Koch 83* (G, US); Northwest plains, 40 km N of Mt. Eba on Stuart Hwy. Watercourse, Sloanes Bore Out Station, *Weber 2972* (NY); WESTERN AUSTRALIA: 34 mi SSE of Turner River Station, *Perry 2416* (BRI, US). **Indonesia.** SUMBA ISLAND: Waingapu (Nambeso), *Expeditie Soemba 37* (BRI); TIMOR: *Riedlé s.n.* (K).

Also reported from India, Burma, and in wool waste in England.

4b. **Malvastrum americanum** (Linnaeus) Torrey var. **stellatum** S. R. Hill, Brittonia **32**(4): 464. 1980. Fig. 30, 31. TYPE: AUSTRALIA. Queensland: Middle Percy Island, 87 mi SE of Mackay, 24 Apr 1956, *M. Lazarides 5606* (HOLOTYPE; BRI!; ISOTYPES; K! US!).

Annual or suffrutescent perennial herb (0.2) 0.4–1 (2) m tall, bushy in age; *main stem* 4–7 mm (or more?) diam at base; *branches* usually 10 30 cm long at maturity, vesture of stem rough in texture, canescent with dense overlapping tufted to appressed sessile (4) 6 7 (8)-rayed stellate hairs 0.2 0.8 mm diam tardily shed; *cotyledons* unknown; *stipules* (3) 5 8 mm long × 0.6 1.0 mm wide, subfalcate, narrowly lanceolate to subulate; petioles (3) 5 20 (30) mm long; *blades* 2.3 5 (7)× longer than the petioles on main stem leaves, (20) 45–60 (75) mm long × (9) 20 30 (35) mm wide, average midstem blade 1.6 2.5× longer than wide to 4.5 × longer than wide in upper leaves, ovate to lanceolate, unlobed or infrequently 3-lobed 1/4 to 1/2-way to the truncate rounded to wide-cuneate base, apex acute to acuminate, margin dentate with 2.5 3.5 (5) teeth/cm, vesture of the adaxial surface of generally overlapping 5 6 (8)-rayed stellate hairs infrequently (*Johnson 1376*) mixed with simple or 2-rayed hairs, 0.8–1.0 mm diam, abaxial surface sparsely to densely pubescent with similar 5–12-rayed hairs; *flowers* overlapping in terminal congested or loosely flowered spikes 2–8 cm long, the first 1 2 (5) infrequently solitary axillary, each flower subtended by a bifid *floral bract* 5–7 mm long × 1.5–2 mm wide divided 1/3 to 1/2 its length; *pedicels* up to 3 mm long to less than 0.5 mm on flowers in spikes, not increasing in fruit; *involucel* of 3 long-acuminate to subulate bracteoles (5) 7–9 (10) mm long × 0.5–1.0 mm wide, generally exceeding the calyx lobes by 1 2 (3) mm in flower, adnate to the calyx in the basal 0.5–1 mm; *calyx* united 1/3 to 1/2 its length, 5 6 mm from pedicel to lobe increasing to 6 9 mm in fruit, campanulate in flower and fruit and indistinctly angled, abaxial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surface densely pubescent or hirsute with apically directed simple to 5-rayed stellate hairs 1.0–1.8 mm diam with minute 6–10-rayed stellate hairs 0.1–0.7 mm diam, with a few minute arachnoid simple or stellate hairs at apex and at margins to sinus; *corolla* ca. 10 mm diam and wide-campanulate to rotate, pale orange-yellow, petals obovate and briefly asymmetrically lobed, ca. 6 mm long × 4 mm wide, exceeding the calyx by 1–2 mm, claws ciliate with tufted simple or stellate hairs 0.5–0.8 mm long; *androecium* with 18–25 (30) stamens, filament tube 1.5-2.0 mm long, pubescent with delicate generally 6-rayed stellate hairs 0.5–0.7 mm diam, free portion of filaments 0.9–1.0 mm long; *gynoecium* with 9–11 (13) carpels, style branching 2–2.5 mm above the columella, each branch terminated by a slightly expanded hemispherical papillate stigma, these generally exserted 0.5-1.0 mm beyond the anthers and recurved at flower wilt; *schizocarps* 4.5–5.5 mm diam; *mericarps* 9–11 (13), 1.6–2.0 mm in height × 2.0–2.5 mm in length × 0.7–0.8 mm wide, distinctly separate from one another, unornamented or with a minute mucro less than 0.1 mm long, faces inconspicuously ribbed, distal-basal surface with a generally inconspicuous raised medial line, distal-apical surface with a shallow sulcus, vesture of apical surface distinctive, with a proximal zone of erect simple hairs ca. 0.5 mm long and a dense medial-distal zone of appressed 6–8-rayed stellate hairs 0.2–0.3 mm diam giving the fruit a frosted appearance, lateral surfaces sparsely pubescent with minute stellate or simple hairs, pericarp chartaceous over the seed and firm to ligneous elsewhere, infrequently partially dehiscent at the base and often dehiscent at the proximal-apical margin, the valves not separating, endoglossum 0.1–0.4 mm long set ca. 0.5 mm distal to

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Figure 30. *Malvastrum americanum* var. *stellatum*. a. Habit, scale = 5 cm. b. Flower bud, scale = 2 mm. c. Mericarp, lateral, internal and apical views, scale = 1 mm. d. Mericarp, lateral, internal and apical views. e. Mericarp, distal view, scale = 1 mm. f. Seed, scale = 1 mm. g. Calyx in fruit (vesture of one lobe only), scale = 2 mm. h. Columella and carpocrater, scale = 0.5 mm. i. Floral bract, adaxial surface, scale = 2 mm. j. Stipule, abaxial surface, scale = 2 mm. k. Bracteole, adaxial surface, scale = 2 mm. l. Midstem leaf, scale = 2 cm. m .Midstem leaf, scale = 2 cm. n. Distal mericarp hair, scale = 0.5 mm. o. Stem hair, scale = 0.5 mm. (a–b, g–k, and o from *Lazarides 5606;* c from *Blake & Everist 3260;* d,f,n from *Johnson 2116;* e from *Lehler & Knowles s.n.*; l from *Johnson 1377A*, m from *Johnson 1376*).

HERBARIO AUSTRALIENSI
Malvastrum striatum A. Gray
M. Lazarides 5806
Middle Percy Island, 87 miles S.E. of Mackay, Q'ld.
Occasional in sandy creek lines.
Erect undershrub to 2 ft. high with yellow flowers.
Malvastrum americanum (L.) Torr.
3rd March, 1976.
S.B.A.
QUEENSLAND HERBARIUM
100662
BRISBANE

the proximal surface; *seeds* ca. 1.5 mm in height × 1.5 mm in length × 0.6 mm wide; *chromosome number:* not known; *pollen* 41–61 (56) μm diam, echinae ca. 4 μm, apertures 6–9.

DISTRIBUTION. (Fig. 32) Australia, in Queensland and New South Wales, most frequent in Leichhardt District, at altitudes of ca. 150–300 meters.

PHENOLOGY AND REPRODUCTIVE BIOLOGY. Collection data indicate that this variety flowers primarily from January until April and less frequently into May and July under favorable conditions. The exserted stigmas suggest outcrossing potential, but the flowers self-pollinate as the stigmas later recurve.

DISCUSSION. This variety is representative of one of the morphological extremes of *Malvastrum americanum* found in Australia. It is more easily recognized as a distinct entity than the others, and may be indigenous to eastern Australia, rather than an ecological variant of a more recently introduced population. The zonation of the apical vesture, the occurrence of dense appressed stellate hairs in that region, in combination with the narrower leaves, usually more loosely-flowered spikes, and more conspicuous bracts and bracteoles serve to distinguish this variety from var. *americanum*.

SPECIMENS EXAMINED: **Australia.** NEW SOUTH WALES: Brewarrina, *Boorman s.n.* (BRI); Hungerford to Brindingabba, *Boorman s.n.* (US); Lightning Ridge, *Constable 19080* (K, pf); 10 km SSW of Camden, Razorback Range, *Coveny et al. 7485* (K); QUEENSLAND: Brisbane, *Bailey s.n.* (MO); Moreton Distr., Toowona, Brisbane, foot of Mt. Coottha, *Blake & Everist 3260* (BRI); Leichhardt Distr., Minerva, *Blake 7948* (BRI); Rockhampton north, State School, *Cleminson s.n.* (BRI); Darling Downs Distr., Toowoomba, *Clydesdale 88* (BRI); Rockhampton, *Dietrich 853 Dietrich s.n.* (US); Blackwater, E of Emerald, *Francis s.n.* (BRI); Imbil, *Fraser 180* (BRI); Leichhardt Distr., 3 mi W of Comet, *Johnson 1376* (BRI, GH) and *1377A* (BRI); Leichhardt Distr., Hillview, 3 mi W of Injune, *Johnson 2116* (BRI); Gympie, *Kenney s.n.* (BRI); Moreton Dist., Hamilton, *Lebler & Knowles s.n.* (BRI); Leichhardt Distr., 12 mi S of Nebo Township, *Story & Yapp 131* (BRI); Maranoa Distr., Mucadilla, *Trenouth 20* (BRI); Mitchell Distr., Gartmore, Tambo, *Wilson 5* (BRI).

5. **Malvastrum chillagoense** K. Domin, Biblioth. Bot. **89**: 386. 1928.
TYPE: AUSTRALIA. Queensland, Cook District, on bare limestone hills, Lion's Head Bluff near Chillagoe, February, 1910. *K. Domin 6499* (LECTOTYPE: PR!). Fig. 33, 34.

Figure 31. *Malvastrum americanum* var. *stellatum* (holotype).

Suffruticose, perennial herb 0.3–3.5 m tall, becoming bushy; *main stem* 3–4 mm diam at base, somewhat woody; *branches* up to 15–25 cm long; *vesture* of somewhat loose and not appressed stellate hairs with 6–8 rays, 0.1–1.2 mm diam; *cotyledons* unknown; *stipules* 2–3.5 mm long × 0.3–0.8 mm wide, linear to narrowly lanceolate on early growth; *blades* (1.5) 3–4 × longer than the petioles, (15) 25–40

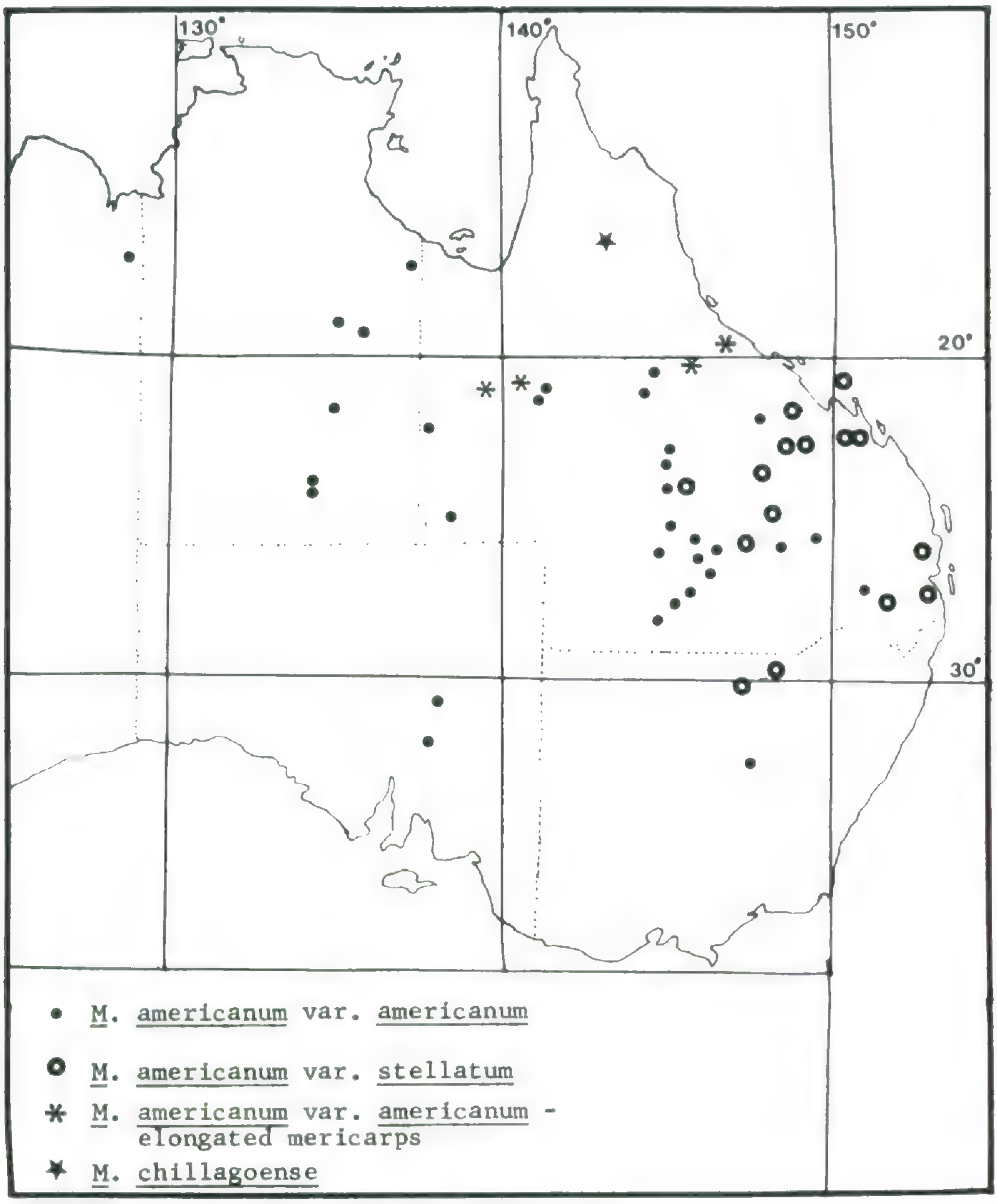
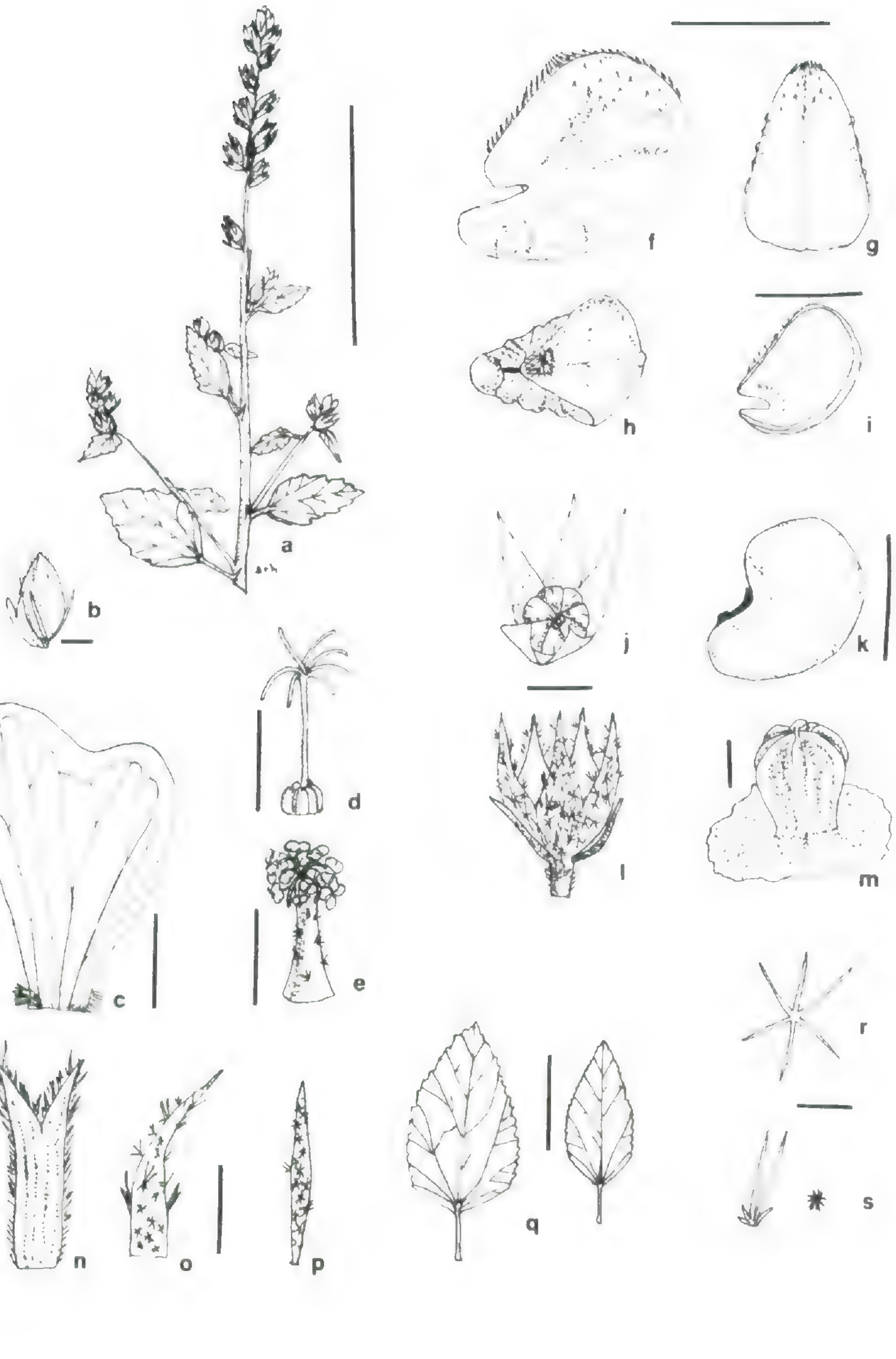


Figure 32. Distribution of *M] americanum* and *M] chillagoense* in Australia.

(1.7) 2–2.2× longer than broad, ovate to ovate-lanceolate, upper leaves narrowest, unlobed, base rounded to broadly cuneate, apex acute, margin dentate with 4–5 teeth/cm, vesture of adaxial surface of somewhat dense 6–8-rayed stellate hairs similar to those of the stem, abaxial pubescence of dense similar 10–12-rayed stellate hairs completely obscuring the surface; *flowers* in axils of leaves, later borne in axils of bifid bracts, infloresence basically an elongated or contracted raceme with reduced spicate floriferous branchlets arising in upper leaf and floral axils; *floral bracts* 3–5 mm long × 1–1.5 mm wide divided 1/3 to 1/2 their length; *pedicels* 1–2 mm long, not increasing in fruit; *involucel* of 3 narrowly lanceolate to linear bracteoles 3–4 mm long × 0.3–0.5 mm wide, free of the calyx; *calyx* united 1/4 to 1/3 its length, campanulate, 5–6 mm long accrescent in fruit to 6–8 mm, lobes narrowly triangular, acuminate, erect in flower and fruit, 3–5 mm long × 1.2–2.1 mm wide, externally tomentose with stellate 6–8-rayed hairs less dense towards apices with a few marginal simple or 2–3-rayed hairs 0.1–1.0 mm diam, lobes arachnoid-pubescent within on upper 1/2; *corolla* yellow or pale orange-yellow, petals asymmetrically bilobed, 6 mm long × 4.5–5 mm wide, exceeding the calyx by 2 mm and campanulate, claw pubescent at the base and margins with rather sparse fine hairs; *androecium* with (20) 23–24 stamens distinctly arranged in 5 rows in bud, filament tube 2.0 mm long, pubescent with sparse fine 3–6-rayed stellate hairs 0.2 mm diam similar in texture to those of the petal claws, free portion of filaments 0.8–1.0 mm long; *gynoecium* with 7 (8) carpels, style 7 (8) branched 2 mm above the columella, each branch with a terminal non-enlarged stigma not exceeding the stamens and generally reflexed in specimens; *schizocarps* 3.5–4.5 mm diam; *mericarps* 7 (8), 1.9 mm in height × 1.2 mm in length × 1 mm in width at the base narrowing toward the apex, unornamented, lateral faces with ribs extending to the thickened distal surface, proximal portion of lateral surface thin over the seed, distal surface with a conspicuous raised medial line, vesture hirtellous, of minute simple hairs 0.2–0.3 mm long restricted to the proximal portion of the apical surface or scattered on the apical margins of the lateral faces, pericarp indehiscent, endoglossum absent; *seeds* 1.2 mm in height × 1.8 mm in length × 0.8–1.0 mm wide; *chromosome number:* not known; *pollen* diam 48.6–64 (57.4) μm, echinae 2.6–3.8 μm, apertures 6–8, usually 7.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DISTRIBUTION. (Fig. 32) Known only from the type locality, limestone bluffs in the vicinity of Chillagoe, Cook District, northern Queensland, Australia, elevation 300–400 m.

PHENOLOGY AND REPRODUCTIVE BIOLOGY. The specimens examined were in flower and with young fruits in February and March, the flowering apparently continuing into April (local autumn). The stigma positions suggest that self-pollination is frequent. The daily flowering time is not known.

DISCUSSION. In several respects, *Malvastrum chillagoense* resembles *M. americanum* var. *americanum* particularly in populations of the latter in north-central Queensland that have a reduced endoglossum, mericarp hairs restricted to the proximal portion of the apical surface, and asymmetrical mericarps (cf. Fig. 27). *Malvastrum chillagoense* differs from these, however, in the fewer and smaller mericarps with their conspicuously ribbed lateral faces as well as by the very different inflorescence structure. Retention of certain primitive characters such as the conspicuous raised medial line of the mericarp, the free bracteoles, the less specialized vesture (particularly on the calyx), and the fairly high frequency of solitary axillary flowers suggest that the ancestor of this species was a more primitive *Malvastrum* and probably not the specialized *M. americanum* as it exists today.

SPECIMENS EXAMINED: **Australia.** QUEENSLAND, Cook District, barren limestone slopes of Lion's Head Bluff near Chillagoe, *Domin 6497* (PR- syntype); among boulders on rugged limestone ridge ca. 1200 ft, Chillagoe, *Blake 13528* (BRI, K).

Section 4. *Tomentosum*

Figure 33. *Malvastrum chillagoense*. a. Habit, scale = 5 cm. b. Flower bud, scale = 2 mm. c. Petal, scale = 2 mm. d. Pistil, scale = 2 mm. e. Stamens, styles, and stigmas, scale = 2 mm. f–h. Mericarp, lateral, distal, apical views, scale = 1 mm. i. Mericarp, internal view, scale = 1 mm. j. Fruit, apical view (vesture of calyx not indicated), scale = 2 mm. k. Seed, lateral view, scale = 1 mm. l. Calyx in fruit, lateral view, scale = 2 mm. m. Columella and carpocrater, scale = 0.5 mm. n. Floral bract, scale = 2 mm. o. Stipule, scale = 2 mm. p. Bracteole, scale = 2 mm. q. Leaves, from midstem and branch apex, scale = 2 cm. r. Stem hair, scale = 0.5 mm. s. Calyx hairs, scale = 0.5 mm. (a–b, j–k, m from *Blake 13528*, c–i, l, n–s from *Domin 6499*).

Figure 34. *Malvastrum chillagoense* (lectotype).

Malvastrum sectio **Tomentosum** S. R. Hill, *sect. nov.*
Carpella matura 9–13, indehiscentia vel margine proximali-apicali dehiscentia, superficie apicali pilis stellatis et simplicibus vel stellatis solis vel glabra, muris lateralibus pericarpii crassis vel coriaceis, cuspidibus 2 distali-apicalibus (0.1–) 0.5–1 (–2) mm longis et cuspide vel interdum mucrone unico proximali-apicali 0.05 0.5 (–1.0) mm longo ornata, marginibus pericarpii angulatis, endoglosso praesenti vel nullo; stamina 25–75, columna staminali pubescenti; flores primo solitarii axillares, demum in racemis terminalibus vel in spicis congestis axillaribus vel terminalibus; bracteolae involucelli basi ad calycem adnatae vel liberae; bractaeae florales bifidae praesentes; pili caulini raro stipatati; pollinis grana aperturis 5–10. Typus: *Malvastrum tomentosum* (L.) S. R. Hill.

The racemose inflorescences, partially dehiscent or indehiscent firm or leathery walled bi- or tricuspidate mericarps, bifid floral bracts, pubescent filament tube, and 5 10 aperturate pollen characterize the section *Tomentosum.*

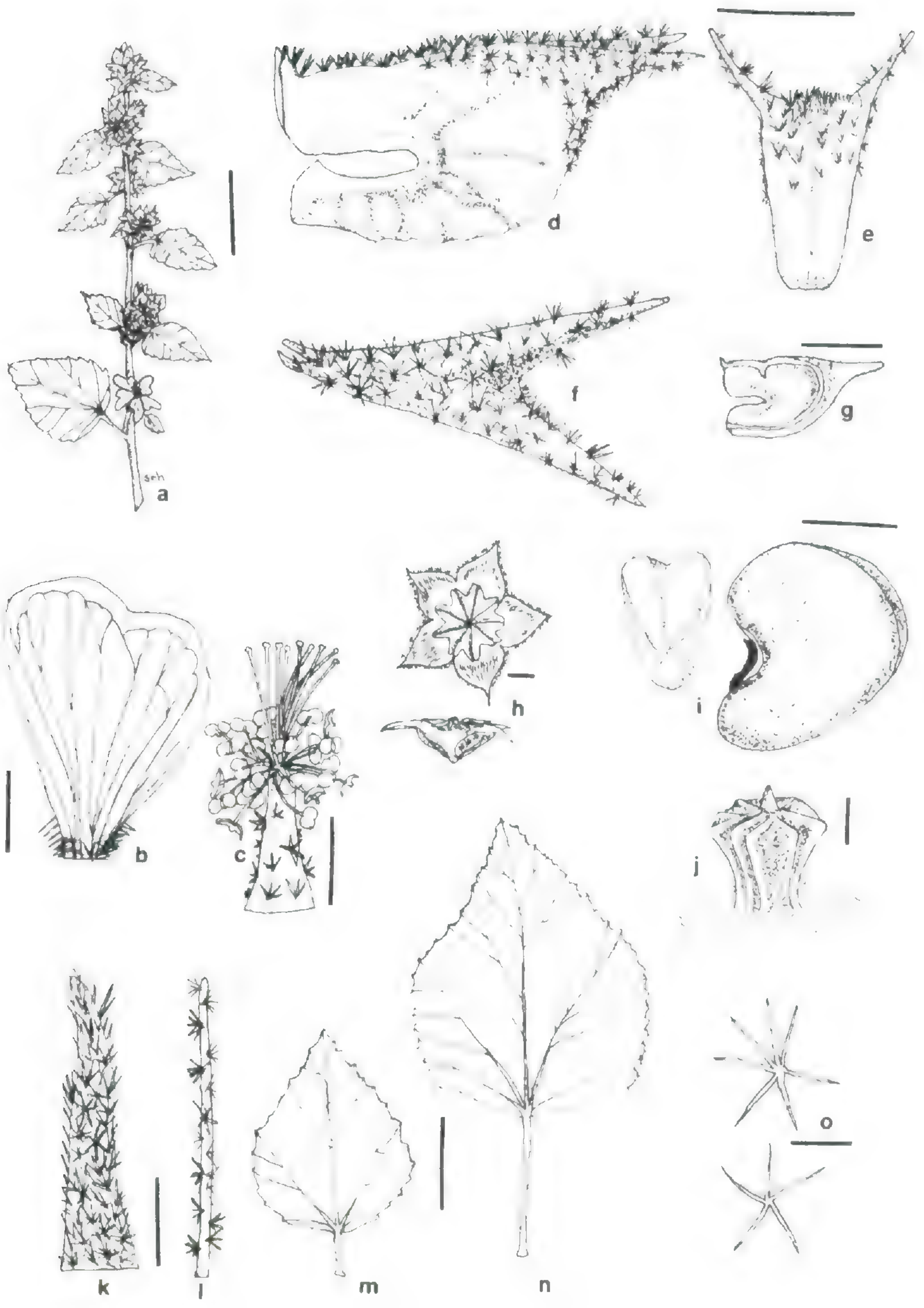
6a. **Malvastrum tomentosum** (Linnaeus) S. R. Hill subsp. **tomentosum,** Brittonia **32**(4): 466. 1980. Fig. 35, 36.

Malva tomentosa Linnaeus, Sp. Pl. **2**: 687. 1753. TYPE: specimen grown at Hortus Upsaliensis, seeds from de Jussieu (LECTOTYPE: LINN No. 870.2).

Malva scoparia L'Héritier, Stirp. Nov. 53, f. 27. 1786, non Jacquin, 1787. TYPE: PERU. Lima: fields at Lima, *Dombey s.n.* (HOLOTYPE: P, fragment at US!; ISOTYPES: BM (no. *95*)!, F (no. *678*)!, MA (no. *678*)). *Malvastrum scoparium* (L'Hérit.) A. Gray, Bot. U.S. Expl. Exped. **1**: 147, in textu. 1854. *Sphaeralcea scoparia* (L'Hérit.) Tidestrom, Proc. Biol. Soc. Wash. **48**: 41. 1935, excl. specim.

Malva scabra Cavanilles, Diss. **5**: 281, t. 138, f. l. 1788. TYPE: cultivated at Hortus Matritensis from seeds from arid regions of Huánuco, Perú, *Cavanilles* (?) *s.n.* (HOLOTYPE: MA (photo-US); ISOTYPES: F!, MA (photo-F), MO!, PH!). *Malvastrum scabrum* (Cav.) A. Gray, Bot. U.S. Expl. Exped. **1**: 147. 1854, excl. specim. et descr. *Malvastrum scabrum* var. *genuinum* E. Hassler, Feddes Repert. Spec. Nov. Regni Veg. **12**: 366. 1913.

Malva waltherifolia Link, Enum. Plant. 209. 1822. TYPE: "Hab. in Java." Link's Berlin types were lost. Ulbrich (1915) examined Link's type, and also cited a specimen in the Bernhardi Herbarium (MO!) which is *Malvastrum tomentosum.* Specimens in the Balbis Herbarium (TO) dated 1823 from Leiden and a specimen at PH! may be isotypes of Link's species. *Anoda waltherifolia* (Link) K. Schumann ex Ulbrich, Feddes Repert. Spec. Nov. Regni Veg. **13**: 510. 1915, pro syn., nom. nud., excl. specim. *Malvastrum waltherifolium* (Link) Ulbrich, Feddes Repert. Spec. Nov. Regni Veg. **13**: 510. 1915.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Sida depressa Bentham, Bot. Sulphur: 69. 1844. TYPE: Isle of Puná near Guayaquil, H.M.S. Sulphur Expedition, *Sinclair s.n.* (HOLOTYPE: K!, ISOTYPES: GH! K!). *Malvastrum depressum* (Bentham) H. K. Svenson, Amer. J. Bot. **33**: 465. 1946.

Malvastrum guaraniticum E. Hassler, Feddes Repert. Spec. Nov. Regni Veg. **12**: 264. 1913. TYPE: BRAZIL: Mato Grosso: Dpt. Bella Vista, in cerrado vegetation near Limeira (formerly in Paraguay), calcareous region above the Río Apa, May 1912/1913. *E. Hassler 11227* (HOLOTYPE: G!, ISOTYPES: A!, BM!, G!, K!).

Malvastrum dimorphum J. T. Howell, Proc. Calif. Acad. Sci. ser. 4, **21**: 331. 1935. TYPE: ECUADOR: Galápagos Islands: Indefatigable Island (Isla Santa Cruz), Academy Bay, 13 May 1932, *J. T. Howell 9294* (HOLOTYPE: CAS no. 220768; ISOTYPE: GH!).

Suffruticose perennial herb 0.6 2.0 m tall often bushy-branched; *main stem* 5–10 mm diam at base with branches up to 30 50 cm long; stem *vesture* canescent-tomentose generally with coarse overlapping (5) 6–7 (8)-rayed stellate hairs 0.3–1.0 mm diam tardily shed in age; *cotyledons* ovate, rounded to slightly emarginate at the apex, wide-cuneate at the base, ca. 9 mm long × 9 mm wide, petiole 6–8 mm long; *stipules* (2) 3–4 (7) mm long × 0.3–0.7 mm wide, narrowly lanceolate to linear, acuminate-cuspidate, subfalcate; *petioles* (15) 25–60 (80) mm long on main leaves to 5–10 mm on apical leaves; *blades* of main stem leaves (1.0) 1.3–1.7 (2.1)× and those associated with the inflorescences 3–5× longer than petioles, main stem leaves (40) 50–85 (115) mm long × (30) 35–75 (90) mm wide and inflorescence leaves (15) 20–45 mm × 10–20 (30) mm, average midstem blade (1.0) 1.1–1.3× longer than wide, ovate and unlobed or very infrequently briefly 3-lobed halfway from the base, base slightly cordate in early leaves to sub-truncate broadly rounded or infrequently broadly cuneate, apex acute or less frequently

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Figure 35. *Malvastrum tomentosum* subsp. *tomentosum*. a. Habit, scale = 5 cm. b. Petal, scale = 2 mm. c. Stamens, styles and stigmas, scale = 2 mm. d–f. Mericarp, lateral, distal and apical views, scale = 1 mm. g. Mericarp, internal view, scale = 1 mm. h. Fruit, apical and lateral views, scale = 2 mm. i. Seed, apical and lateral views, scale = 1 mm. j. Columella and carpocrater, scale = 0.5 mm. k. Stipule, scale = 1 mm. l. Bracteole, scale = 1 mm. m. Leaf from branch apex, scale = 2 cm. n. Leaf, midstem, scale = 2 cm. o. Stem hairs, scale = 0.5 mm. (a–c, j from *Camp E-2974;* d–f, l from *Stork, et al. 8973*; g, i from *Macbride 531;* h from *Weberbauer 7760;* k from *Rose 22548;* m from *Eggers 15778;* n from *Asplund 15688;* o from *Smyth 57*).

Figure 36. *Malvastrum tomentosum* subsp. *tomentosum* (lectotype).

slightly acuminate, margin crenate-dentate to dentate or nearly denticulate in upper leaves with 2.5–4 (6) teeth/cm, vesture of adaxial surface felty to slighty rough, of overlapping and often dense appressed symmetrical 6–8-rayed stellate hairs similar to those of the stem, abaxial surface pubescent-canescent and obscured by scarcely appressed 8–12-rayed stellate hairs 0.5–0.8 mm diam; *flowers* at first solitary in the axils of leaves and stipules, later congested and subtended by paired stipules and a highly reduced leaf 1 2 mm long in reduced few-flowered axillary and terminal glomerate spicate racemes, these units present on both main and secondary stems on older plants, bifid *floral bracts* lacking; *pedicels* 2.0–4.0 (15) mm long on axillary flowers and 0.5–1.0 mm long on the congested flowers, not increasing in fruit; *involucel* of 3 filiform bracteoles 3–4 (–5) mm long × 0.2–0.4 mm wide, completely free of the calyx; *calyx* united 1/3 its length, 4–5 (6) mm long at anthesis increasing to 6–8 (11) mm in fruit, campanulate in flower and typically rotate in fruit, lobes triangular to deltate, acuminate-cuspidate or infrequently broadly cuspidate to subacute, 3–4 (5) mm long × 2 3 mm wide at anthesis to 5–6 (8) mm long × 3–4.5 (5.0) mm wide in fruit, abaxial surface canescent with 4–8-rayed stellate or infrequently simple marginal hairs 0.1–0.5 mm diam usually obscuring the surface, adaxial surface of lobes downy-pubescent with minute arachnoid hairs on the apical half and marginally to the lobe sinus, usually strigose medially with simple or 2-rayed apically directed hairs 0.2 0.7 mm long; *corolla* (10–) 15–18 mm diam, orange-yellow to pale orange, petals asymmetrically bilobed, 6 7 (9) mm long × (3) 4 5 (7) mm wide (usually shrinking upon drying in pressed specimens), broadly campanulate and spreading at anthesis, exceeding the calyx by 2 3.5 mm, claws densely strigose-pubescent throughout to somewhat barbate with 2–4-rayed or simple hairs 0.2–0.5 mm long; *androecium* with (25) 34–38 (42) stamens, filament tube 2.5–3.0 mm long, moderately pubescent with 2 5-rayed stellate hairs 0.2–0.6 mm diam, free portion of filaments 0.9 1.4 mm long; *gynoecium* with (9) 10 12 (13) carpels, style branching 2.5 3.0 mm above the columella, each branch terminated by a single only slightly expanded sub-hemispherical stigma exserted 1.0 1.5 (2.0) mm beyond the anthers but often recurved in pressed specimens; *schizocarps* (5.5) 6.0–8.0 (9.0) mm diam including ornamentation; *mericarps* (9) 10–12 (13), appressed to slightly remote from one another at maturity, 2.0 3.0 mm in height × 2.5 4.0 mm in length ×

1.0–1.2 mm in width including ornamentation, with a single proximal-apical cusp (0.1) 0.2 0.5 (1.0) mm long and two conspicuous distal-apical cusps 0.8–1.8 (2.0) mm long, lateral faces somewhat smooth to conspicuously ribbed without a prolonged concave margin, raised midline present on the distal-apical surface but usually obscured apically by hairs, densely pubescent on the apical surface with tufted 8 10-rayed stellate hairs and a few simple erect hairs 0.1–0.4 mm long on the proximal cusp, the proximal-apical hairs often with 2–3 elongated ascending rays, mericarp indehiscent except for an open proximal-apical margin, lateral faces of the pericarp thin over the seed but firm to woody elsewhere, endoglossum 0.2 0.3 mm long on the apical surface 0.5 mm distal to the open proximal margin; *seeds* 1.5 mm in height × 1.8–2.0 mm in length × 0.8 1.0 mm in width, with a longitudinal cleft in the distal-apical region corresponding to the cusps on the mericarp; *chromosome number*: $n = 12$, $2n = 24$; *pollen* 46–77 (60) μm diam, echinae 3–6 μm, apertures 6–9 (10).

DISTRIBUTION. (Fig. 37) Moderate elevations in brushland in well-drained or dry soils surrounding the Amazon basin, most frequently in coastal regions from the Department of Ica, Peru in the south to the Province of Manabí, Ecuador in the north, with disjunct populations in the Distr. Federal and State of Aragua, Venezuela, and in the states of Ceará, Paraiba, Pernambuco, Minas Gerais, and Matto Grosso in Brazil, at elevations from near sea level to 1500 m.

PHENOLOGY AND REPRODUCTIVE BIOLOGY. Flowering (in wild populations) primarily from April to late June, but also sporadically throughout the year under proper conditions. Greenhouse plants grown from seeds from *Stork et al. 8973*, *Iltis 1591*, and *da Rocha 3* (40 years old) germinated in 1 3 weeks after planting and were in bud in early November after 6 months (180 days) growth, but did not flower well and became dormant or died in winter greenhouse conditions (as low as 2°–7° C at night). The plants were seen to grow best in warm, dry conditions. Flowering time and breeding mechanisms are unknown, but it is suspected that self-pollination mechanisms are well-developed due to the recurved styles often seen in pressed specimens and the nearly 100% fruit set.

DISCUSSION. For a detailed discussion of nomenclature in this species see Hill (1980).

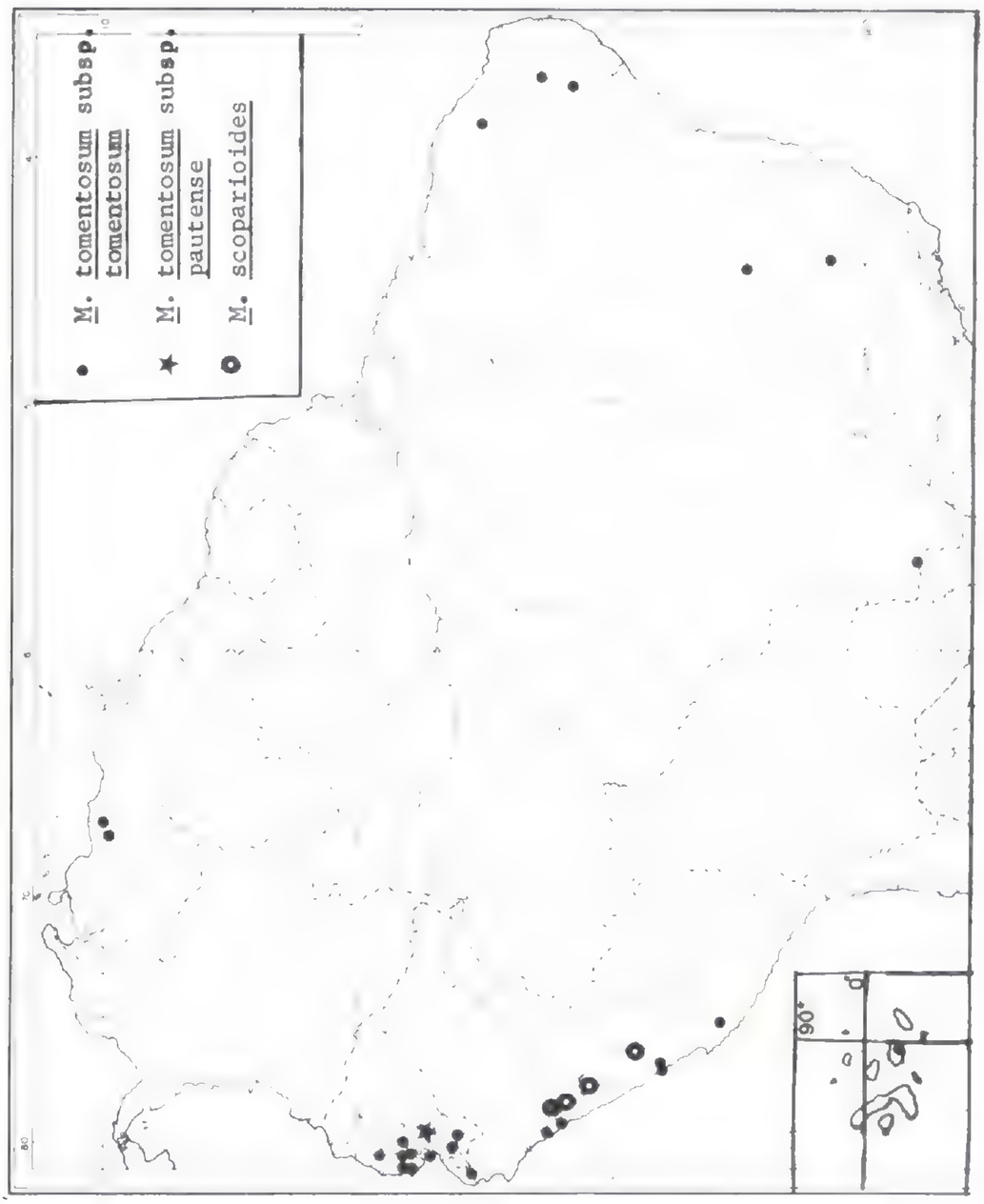

Figure 37. Distribution of *Malvastrum tomentosum* and *M. scoparioides*. Inset: Galápagos Islands.

REPRESENTATIVE SPECIMENS: **Venezuela.** ARAGUA: Colonia Tovar, *Fendler 88* (G, GH, K, NY, PH); DISTRITO FEDERAL: between Antimano and Las Adjuntas, *Pittier 12254* (G, NY, US). **Ecuador.** MANABÍ: El Recreo, *Eggers 15778* (F, K, US); GUAYAS: Guayaquil, *Hitchcock 19935* (GH, NY, US); 8 km N of Guayaquil, dry hillside, *Stork et al. 8973* (K, UC, US); ISLAND OF PUNÁ: H.M.S. Sulphur Expdition, *Sinclair s.n.* (GH, K); LOS RÍOS: Vinces, collector not indicated, (GH); CHIMBORAZO: Huigra, Hacienda de Licay, *Rose et al. 23886* (GH, NY, US); cañon of the río Chanchan near Huigra, *Camp E-2974* (CAS, F, GH, K, MO, NY, US); EL ORO: Santa Rosa, *Asplund 15688* (B, NY); LOJA: Catamayo Valley near La Toma (Catamayo) *Wiggins 10955* (CAS, DS, MO); GALÁPAGOS ISLANDS: Indefatigable Island (Santa Cruz), Academy Bay, Pelican Bay, *Schimpff 35* (BKL, CAS, G, GH, MO, NY, U); Academy Bay, *Howell 9294* (CAS, GH). **Peru** PIURA: Prov. Paita, La Brea, *Weberbauer 7760* (F); CAJAMARCA: Prov. Cutervo, Izco, *Stork & Horton 10208* (F, UC); LA LIBERTAD: Chicama Valley, cultivated fields, *Smyth 57* (US); LAMBAYEQUE: mouth of the río Chancay, *Spruce 6390* (BM, G, K, OXF); LIMA: Chosica, in river gravel, *Macbride & Featherstone 531* (F, G, GH); ICA: Prov. of Nazca, Nazca, *Iltis et al. 1591* (BH, WIS). **Brazil.** BAHÍA: Brejoes, Estrada BR. 4, *Krapovickas 12785* (MICH, UC); CEARÁ: *da Rocha 3* (US); PARAIBA: fields in Areia, *Moraes 810* (NY, U); PERNAMBUCO: Tapera, *Pickel 3751* (GH, NY); MINAS GERAIS: 1 km E of río Pandeiros, road to Januária, *Anderson et al. 9099* (NY, pf, UB); MATTO GROSSO: Dpto. Bella Vista, near Limeira, above the río Apa, *Hassler 11227* (A, G).

6b. **Malvastrum tomentosum** (Linnaeus) S. R. Hill subsp. **pautense** S. R. Hill, Brittonia **32**(4): 470. 1980 TYPE: ECUADOR, Azuay: dry hillsides along roadside in valley of Río Paute, alt. ca. 7700 ft, 24 Sept. 1944, *I. L. Wiggins 10788* (HOLOTYPE: GH!; ISOTYPES: CAS!, DS!, NY!, TEX!, US!). Fig. 38, 39.

Similar to the typical subspecies in most respects, but differing in its campanulate calyces with incurved and not patent lobes in fruit, in the shorter distal cusps which are 0.5–0.7 mm long, inthe larger stellate hairs on the apical surface that are 0.5–0.7 mm long and generally have several elongate, centrally directed rays, in the very inconspicuous endoglossum, and in the absence of the sulcus that is present on the seeds of the typical subspecies. The leaves seem to be more frequently trilobed than in subsp. *tomentosum; chromosome number:* not known; pollen: 77–90 (84) μm diam, echinae 4–5 μm, aperatures 7–10.

DISTRIBUTION. (Fig. 37) Restricted to the region of the río Paute, Province of Azuay, Ecuador, on dry cliffs and rocky hillsides at elevations of 2400–2700 m.

PHENOLOGY AND REPRODUCTIVE BIOLOGY. Flowering in September and again in March and April. A plant grown from seed from the

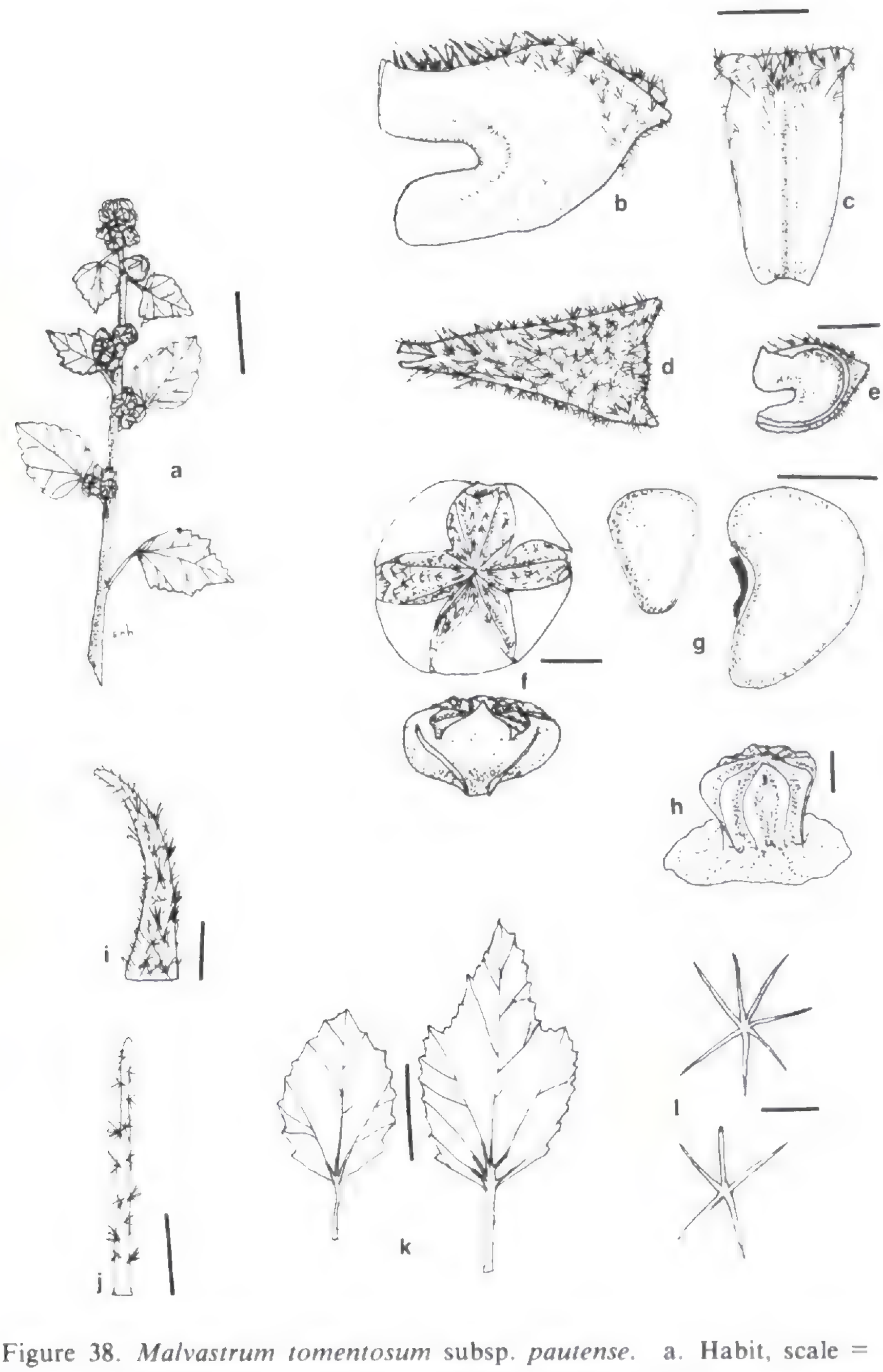

Figure 38. *Malvastrum tomentosum* subsp. *pautense*. a. Habit, scale = 5 cm. b–d. Mericarp, lateral, distal and apical views, scale = 1 mm. e. Mericarp, internal view, scale = 1 mm. f. Fruit, apical and lateral views, excluding vesture, scale = 2 mm. g. Seed, scale = 1 mm. h. Columella and carpocrater, scale = 0.5 mm. i. Stipule, abaxial surface, scale = 1 mm. j. Bracteole, abaxial surface, scale = 1 mm. k. Leaf variation, apical leaves, scale = 1 cm. l. Stem hairs, scale = 0.5 mm. (a,f,h–l from *Camp E-2542;* b–e and g from *Wiggins 10788*).

type (*Wiggins 10788*, 34 years old) grew poorly in the warm greenhouse temperatures in Texas, germinating 35 days after planting, and produced two flowers in September (after ca. 100 days of growth) that self-pollinated to produce two fruits. In the winter months the plant became dormant but remained green while plants of the typical subspecies died from the nearly freezing temperatures.

DISCUSSION. During the examination of specimens of *M. tomentosum* a small set of unusual forms was set aside. Upon re-examination, it was seen that these "atypical" specimens not only had a morphic continuity with one another but also originated in a single province (Azuay) in Ecuador at elevations greatly exceeding those of the species overall. These considerations led me to treat this population as a new subspecies of *M. tomentosum*. It is interesting that this population that is so near to the frequency center of the species is much more divergent in its characters than are the isolated populations of the species in Venezuela and Brazil.

It is my view that the two subspecies are effectively isolated from one another. Since isolation in the río Paute basin, selective pressures to maintain the mericarp cusps for transport have probably lessened. The plants seem also to have adapted physiologically to the cooler temperatures of the higher elevations.

SPECIMENS EXAMINED: **Ecuador.** AZUAY: Dry hillsides, valley of the río Paute, *Wiggins 10788* (CAS, DS, GH, NY, TEX, US); between ríos Azogues and Gualaceo, valley of the río Paute between Paute and Cuenca, Camp *E-2339* (CAS, G, NY) and *E-2542* (CAS, NY, UC).

7. **Malvastrum scoparioides** E. Ulbrich, Notizbl. Königl. Bot. Gart. Berlin **11**: 525. 1932. TYPE: PERU: Ancash: Prov. Huailas, beyond Pamparomas, between Samanco and Caras, woodland near brook, altitude 2000–2200 meters, May 29, 1903. *A. Weberbauer 3196* (HOLOTYPE: B — (lost) fragment at CAS!; ISOTYPE: MOL). Fig. 40, 41.

Malvastrum scabrum sensu A. Gray, Bot. U. S. Expl. Exped. **1**: 147. 1854, excl. basionym. Applied to a specimen collected on the Wilkes Expedition (US!) which is this species and which Gray considered to be the *Malva scabra* of Cavanilles.

Figure 39. *Malvastrum tomentosum* subsp. *pautense* (holotype).

DUDLEY HERBARIUM OF STANFORD UNIVERSITY
Plants of Ecuador
alvastrum scoparium (D'Her.) A. Gray?
Kearney 1952)
Shrub to about 2 m. branches straggly.
Flowers pale orange.
dry hillsides along roadside in valley
of Rio Paute, alt. about 7,700 ft.
Ira L. Wiggins
1944

Suffruticose to subarborescent perennial herb 1–3 m tall, sparsely branched the first year, later bushy-branched; *main stem* 10 (15) mm diam at base; *branches* to 30–45 cm long; *vesture* of scattered appressed (4) 5–6 (7)-rayed stellate hairs 0.3–0.9 mm diam persistent or tardily shed; *cotyledons* wide-ovate, apex briefly emarginate, base truncate to broadly cuneate, 10–11 mm long × 11 mm wide; *stipules* 3–4 (5) mm long × 0.7–0.9 mm wide, narrowly lanceolate to linear, acuminate-cuspidate, subfalcate; *petioles* 35 70 (100) mm long to 5–15 mm in inflorescence leaves; *blades* of lower leaves 1.5–3.0× and those associated with the inflorescence 4 6.5× longer than petioles, lower blades 65–90 (125) mm long × 50–85 (90) mm wide, those with the inflorescence (25) 30 40 (60) mm long × 20 25 mm wide, average midstem blade 1.3 1.6× longer than wide, ovate, usually unlobed but infrequently briefly 3-lobed halfway from the base, base cordate to rounded or wide-cuneate, apex acute to acuminate, gradually tapering from the middle, margin coarsely dentate to denticulate with 1–2 to 5 teeth/cm, vesture of the adaxial surface of scattered (5) 6 (7)-rayed hairs 0.2 0.9 mm diam or simple towards the margins, occasionally with 2 or 3 elongated marginally directed rays, abaxial surface more densely pubescent with fine scarcely appressed (6) 8–10-rayed stellate hairs 0.5 0.8 mm diam; *flowers* solitary in the axils of reduced leaves and stipules at first, later in congested reduced terminal and axillary few-flowered racemes and subtended by paired stipules and minute leaf or a bifid *floral bract* 5.5–6.0 mm long × 1.0–1.2 mm wide divided 2/3 to 5/6 its length; *pedicels* 0.7 1.0 (4.0) mm at anthesis increasing by less than 1 mm in fruit; *involucel* of 3 filiform bracteoles 4–5 mm long × 0.3–0.5 mm wide completely free of the calyx; *calyx* united 1/3 to 3/5 its length, 8–9 mm long at anthesis to 10–11 mm in fruit,

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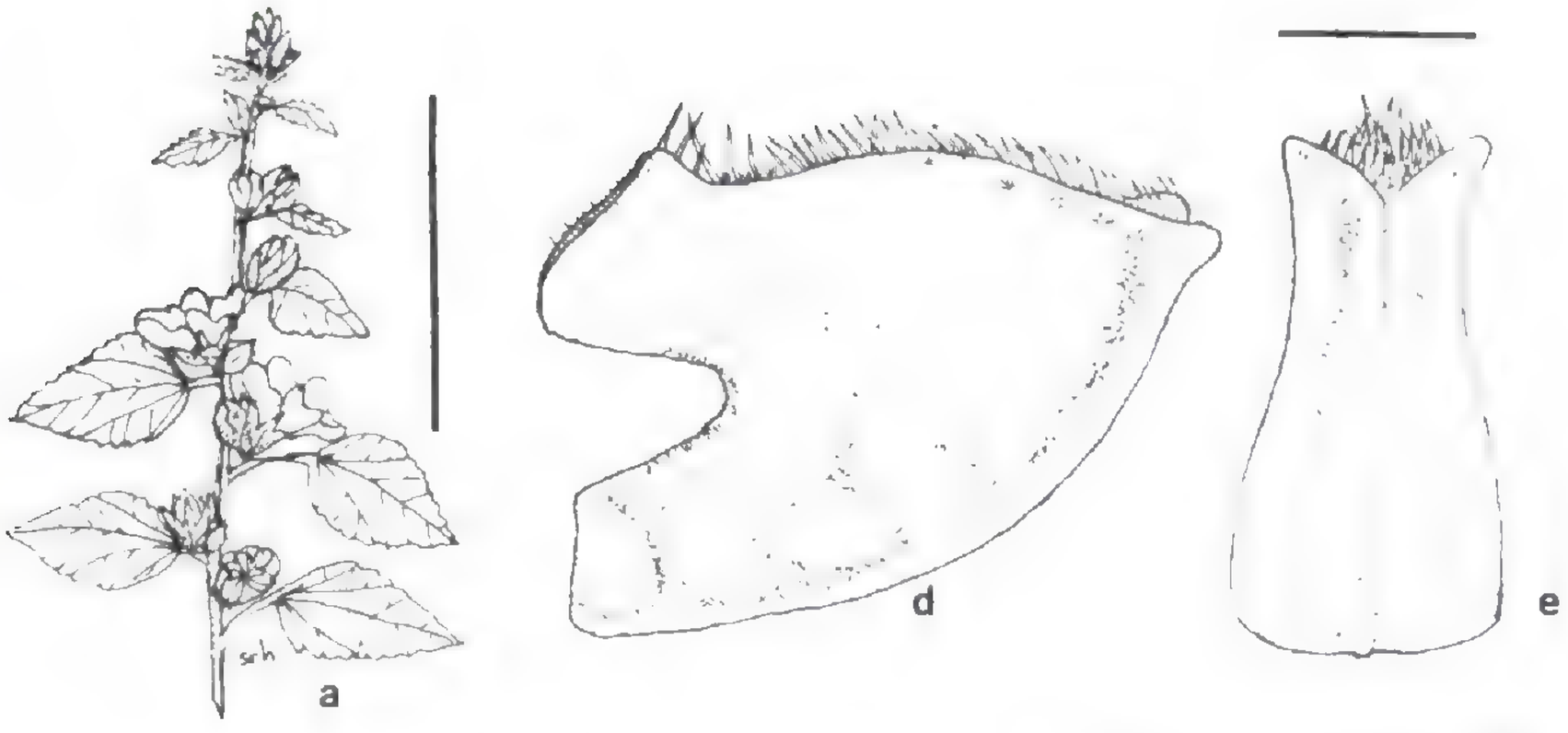
Figure 40. *Malvastrum scoparioides*. a. Habit, scale = 5 cm. b. Petal, scale = 2 mm. c. Stamens, styles, and stigmas, stigma enlarged, scale = 2 mm. d.–f. Mericarp, lateral, distal, and apical views, scale = 1 mm. g. Mericarp, internal view, scale = 1 mm. h. Fruit, apical view, without vesture, scale = 2 mm. i. Seed, scale = 1 mm. j. Calyx at anthesis, scale = 2 mm. k. Columella and carpocrater, scale = 0.5 mm. l. Floral bracts, fully developed and transitional forms, scale = 2 mm. m. Stipule, scale = 2 mm. n .Bracteole, scale = 2 mm. o. Midstem leaf, scale = 2 cm. p. Cotyledon, scale = 5 mm. q. Stem and leaf hairs, scale = 0.5 mm. r. Mericarp hairs, scale = 0.5 mm. (all from living and cultivated specimens of *López-M & Sagástequi-A. 8020).*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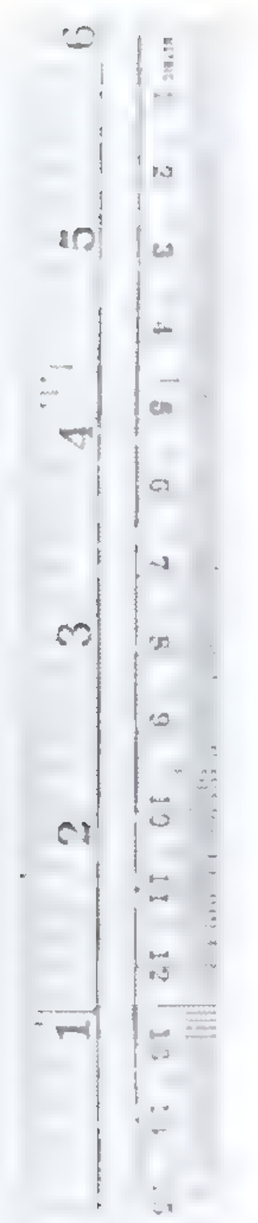
campanulate, lobes slightly spreading at anthesis and erect to incurved in fruit, triangular, acuminate-cuspidate, 5 mm long × 3–4 mm wide to 7 mm long × 4 5 mm wide in fruit, abaxial surface canescent with minute simple to 6-rayed stellate hairs 0.05 0.2 mm diam and similar larger stellate hairs 0.5 0.7 mm in diam, adaxial surface of lobes conspicuously downy pubescent with minute simple or 2-rayed arachnoid hairs on the apical 1/2 and marginally to the lobe sinus; *corolla* pale orange, 23 24 mm diam when spread, petals asymmetrically bilobed, 10-11 (13) mm long × 9 10 mm wide, broadly campanulate or spreading and exceeding the calyx by 4 5 (6) mm, claws densely barbate-pubescent with fine simple or 2 4-rayed stellate hairs 0.8-1.0 mm long; *androecium* with 36 46 stamens, filament tube 4.0 mm long, sparsely pubescent with 2 5-rayed stellate hairs 0.8-1.0 mm diam, free portion of filaments 1.0–1.5 mm long; *gynoecium* with (10) 11–12 carpels, style branching 3.5 4.0 mm above the columella, each branch terminated by an expanded somewhat flattened subhemispherical to discoid stigma exserted 2 mm beyond the anthers, not recurved at flower wilt; *schizocarps* 8 9 mm diam including ornamentation; *mericarps* (10) 11 12, divergent at maturity, 2.5–3.0 mm in height × 3.5 4.0 mm in length including ornamentation × 1.2 1.6 mm in width, with a minute apical cusp 0.05–0.2 mm long and two apical-distal cusps 0.3–0.6 mm long, lateral faces smooth or inconspicuously ribbed at the distal and basal margins which are narrowly prolonged to form a concave rim, distal and basal surfaces with a conspicuous raised medial line, vesture restricted to the apical surface and the extreme apical margin of the lateral surfaces consisting of appressed proximally-directed simple hairs 0.5 0.8 mm long mixed with minute stellate hairs ca. 0.1 mm diam, mericarp proximal-apical margin usually unsealed at maturity, lateral portion of pericarp over the seed thin and chartaceous the remainder somewhat woody, minute endoglossum present on the apical surface 1.0 mm distal to proximal margin, tardily separating from the receptacle; *seeds* 2.0 mm in height × 2.2 mm in length × 1.0 mm in width; *chromosome number:* $2n$ = ca. 48; *pollen* 67–93 (76) μm diam, echinae 5 μm, apertures 10–18.

Figure 41. *Malvastrum scoparioides* (holotype photo, and fragment, CAS).



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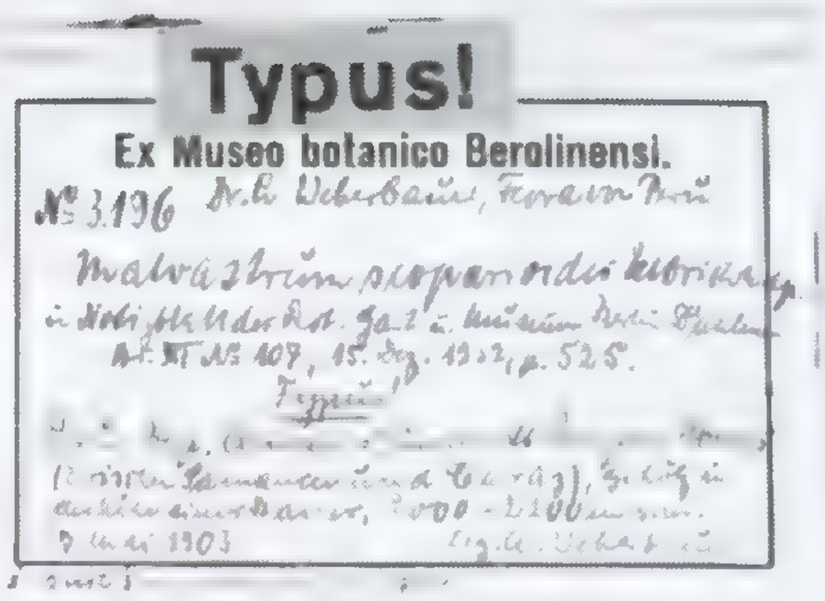
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DISTRIBUTION. (Fig. 37) Restricted to hillsides and slopes in the Departments of southern Cajamarca, La Libertad, Ancash and northern Lima, Peru, at moderately high elevations of 1300–2200 m.

PHENOLOGY AND REPRODUCTIVE BIOLOGY. Flowering in April and May, but has also been collected in flower and fruit in early September. Greenhouse plants grown from seeds from *López-M. & Sagástegui-A. 8020* (five years old) germinated in two weeks after planting and flowered for the first time in January after eight months growth. The plants grew slowly in the summer months in elevated temperatures (29° 39° C) but well in the cooler weather in the greenhouse while the *Malvastrum tomentosum* plants were becoming dormant or moribund. The flowers opened at 11 am CST and closed at 4:30 5 pm CST. The stigmas remained exserted throughout and did not recurve preventing pollination. Self-pollination failed to produce fruit.

DISCUSSION. *Malvastrum scoparioides* has been confused with *Malva scabra* Cavanilles (*Malvastrum scabrum* (Cav.) A. Gray) which has similar leaves. However, the larger flowers, presence of bifid bracts, the reduced cusps, the vesture of simple hairs on the mericarp, and the divergence of the mericarps in fruit separate *M. scoparioides* from *M. tomentosum*. A tentative root tip chromosome count suggests that this is a polyploid species, possibly an octoploid. If so, this would be the second octoploid known in the genus. The occurrence of the species at high altitudes is correlated with the higher ploidal level.

In cultivation, individuals of this species were better able to withstand nearly freezing winter temperatures and were more resistant to insect and fungal predation than were individuals of *Malvastrum tomentosum*. Warm summer temperatures discouraged

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Figure 42. *Malvastrum guatemalense*. a. Habit, scale = 5 cm. b. Stem vesture, scale = 0.5 mm. c. Petal, scale = 2 mm. d. Stamens, styles, and stigmas, scale = 2 mm. e.–g. Mericarp, lateral, distal, and apical views, scale = 1 mm. h. Mericarp, internal view, scale = 1 mm. i. Fruit, apical view, scale = 2 mm. j. Seed, lateral and apical views, scale = 1 mm. k. Calyx and bract at anthesis, scale = 2 mm. l. Columella and carpocrater, scale = 0.5 mm. m. Stipule, scale = 1 mm. n. Bracteole, scale = 1 mm. o. Floral bract, scale = 1 mm. p. Leaf, scale = 2 cm. q. Vesture variation: 1) calyx, 2) leaf, abaxial surface, 3) leaf, adaxial surface, 4) mericarp, scale = 0.5 mm. (a,d,i,l from *Standley 77661;* b, from *Williams & Molina 10865*, c,k,m–n, p–q from *Standley 78534*, e–h,j,o from *Williams, et al. 23821*).

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flowering. *Malvastrum scoparioides* is interpreted to be a polyploid derivative of *M. tomentosum,* physiologically, cytologically, and ecologically isolated from contemporary populations of that species. Convergence in characters resulting in a coincidental similarity with *M. tomentosum* subsp. *pautense* seems to have taken place as a result of an adaptation to a very similar habitat.

SPECIMENS EXAMINED. **Peru.** CAJAMARCA: Prov. Contumazá, Cascas - Contumazá, hillside, *López-M. & Sagástegui-A. 7672* (MO, pf, US); LA LIBERTAD: Prov. Otuzco, Hda. Membrillar, *López-M. 596* (US); Prov. Otuzco, road from Simbel to La Cuesta, *López-M. & Sagástegui-A. 8020* (F, GH, MO, NY); ANCASH: Prov. of Huailas, beyond Pampa-romas, between Samanco and Caras, *Weberbauer 3196* (CAS); LIMA: Prov. of Canta, Obrajillo, *Wilkes Expedition s.n.* (US).

8. **Malvastrum guatemalense** Standley & Steyermark, Publ. Field Mus. Nat. Hist., Bot. Ser. **23**: 174. 1944. TYPE: GUATEMALA. Santa Rosa, near Cuilapa, in wet thicket, alt. 900 meters, November 20–27, 1940. *P. C. Standley 78534* (HOLOTYPE; F!). Fig. 42, 43.

Suffruticose, perennial herb to 2 m tall, apparently sparsely branched; *mid-stem* diam 5 mm; *branches* to 50 cm long, vesture sparse, consisting of minute simple hairs 0.1 0.2 mm long perpendicular to the stem and appressed (2) 4 5 (6)-rayed stellate hairs (0.2) 1 1.5 (2.0) mm diam; *cotyledons* not known; *stipules* 4 5 mm long × 0.6 0.8 mm wide, narrowly lanceolate to linear; *petioles* (20) 40 50 mm long; *blades* 1.4 -2× longer than the petioles (30) 60 75 (90) mm long × (25) 35 55 (60) mm wide, average midstem blade 1.3 1.5× longer than broad, ovate wide-ovate to elliptic, unlobed or minutely 3-lobed 2/3 the distance from the rounded to broadly cuneate base, apex acute, margin crenate-dentate with 3–4 teeth/cm, vesture of the adaxial surface consisting of scattered evenly arranged apically directed simple hairs 1.5 mm long, abaxial pubescence of 6–12-rayed stellate hairs 0.4 1.0 mm diam; *flowers* typically in loosely flowered terminal racemes and in reduced axillary racemes in the axils of upper leaves and stipules or subtended by *floral bracts* 3 4 mm long × 0.8 1.0 mm wide; *pedicels* 1 2 (4) mm long, increasing about 1 mm in fruit; *involucel* of 3 lanceolate bracteoles 5 7 mm long × 0.6–0.8 mm wide, united to the calyx 1.5–2.0 mm at base; *calyx* united 1 4 to 1 3 its length, somewhat campanulate, 6 8 mm long to 8 11 mm in fruit, lobes only slightly spreading in flower and

Figure 43. *Malvastrum guatemalense* (holotype).

fruit, narrowly triangular, acuminate, 5-7 (9) mm long × 2-4 mm wide, strigose on the outside with coarse simple hairs 1–1.5 mm long occasional 2–5-rayed hairs and appressed minute stellate hairs 0.1–0.3 mm diam covering the remaining surface, internal surface of lobes downy pubescent with minute arachnoid hairs on the upper two-thirds; *corolla* pale yellow or yellow orange, petals asymmetrically bilobed, 7–9 mm long × 6 mm wide, spreading at anthesis, exceeding the calyx by 2–3 mm, claw pubescent at base with rather dense stellate and simple hairs; *androecium* with 38 44 stamens, filament tube 2–2.5 mm long, pubescent with fine 2–6-rayed stellate hairs resembling those of the claws, free portion of filaments 1.0 mm long; *gynoecium* with 9–10 carpels, style branching 2 mm above the base into 9–10 branches, each with a single terminal hemispherical expanded stigma exceeding the anthers by 1–1.5 mm; *schizocarps* 4.5–6.0 mm diam; *mericarps* 9–10 (usually 10), 2 mm in height × 3 mm in length (including ornamentation) × 1.0 mm in width excluding hairs, with two distinctly separate distal-apical cusps 0.5 mm long, lateral faces unribbed, vesture of the apical surface of small stellate hairs 0.1-0.4 mm diam mixed with large rigid simple hairs 1.0 mm long with intermediates, lateral margins with a distinctive dense vesture of small simple bristle-like hairs 0.3 mm long perpendicular to the faces forming a thick brush, pericarp indehiscent, endoglossum lacking, apparently readily separating from the receptacle at maturity; *seeds* 1.5 mm in height × 2 mm in length × 1 mm in width with a noticeable sulcus on the apical-distal surface; *chromosome number:* not known; *pollen:* 71.7–79.4 (74.7) μm diam, echinae 2.5–5 μm, apertures 6–7.

DISTRIBUTION. (Fig. 44) Known from forested regions of Guatemala, Honduras, and Nicaragua at elevations of 600–1200 m.

PHENOLOGY AND REPRODUCTIVE BIOLOGY. Flowering in late October–January. The exserted stigmas suggest that effective cross-pollination is possible. Daily flowering time not known.

DISCUSSION. There remains some question whether *M. guatemalense* should be considered a distinct species or another subspecies of *M. bicuspidatum*. I have retained it in the rank of species on the basis of its disjunct range (the subspecies under consideration have contiguous ranges), as well as on the basis of

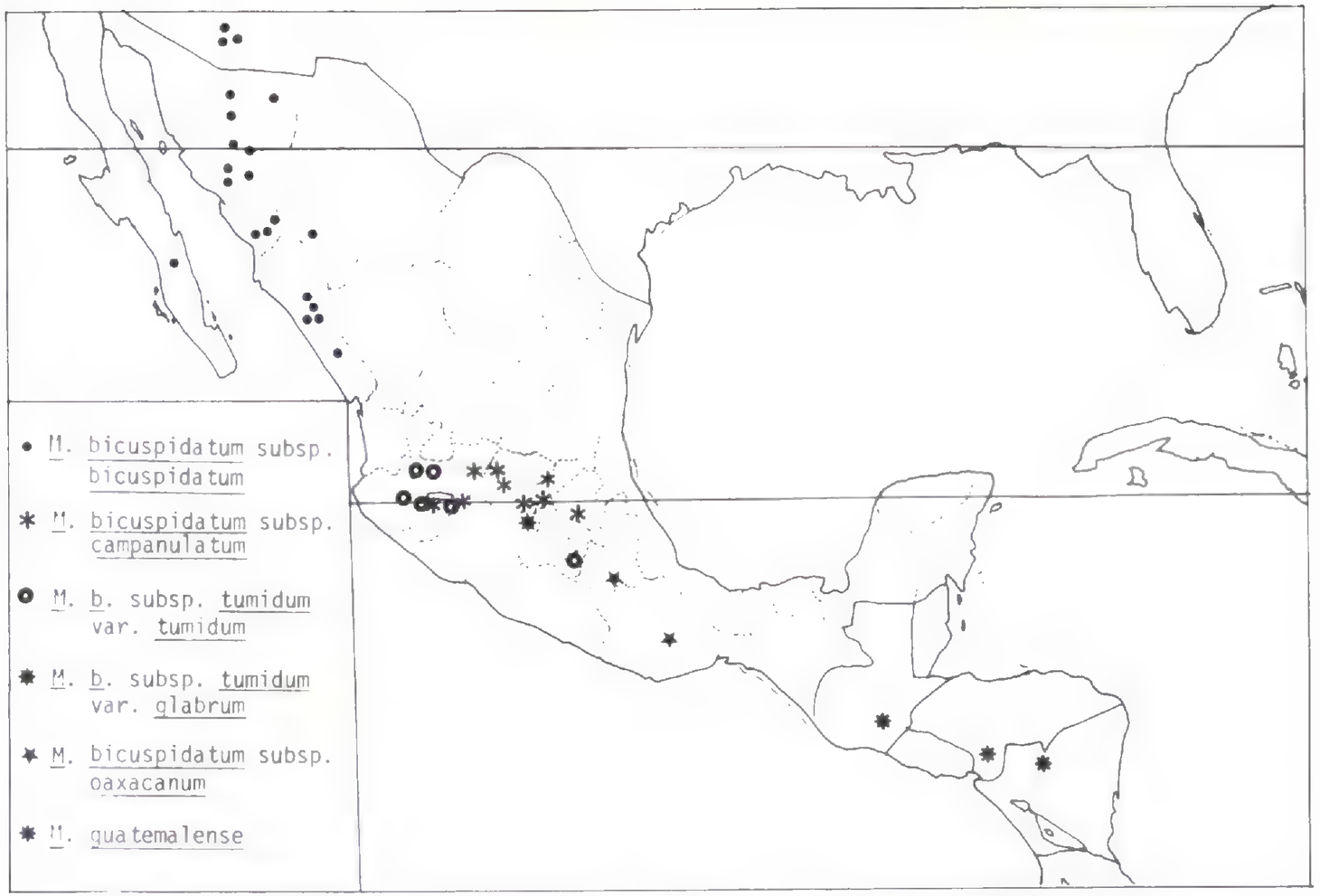

Figure 44. Distribution of *Malvastrum* section *Tomentosum* in North America.

several morphic features that do not occur in *M. bicuspidatum* (e.g. the unusual vesture characters of the mericarps and stems).Numerical data presented in Appendix II suggest that *M. guatemalense* is more closely allied with *M. bicuspidatum* subsp. *tumidum* than that taxon is with the other subspecies of *M. bicuspidatum*. Surely the two are very close, but most of the similarities are those of a reductional or derived nature, or pertain to ecologically adaptive vegetative features; the mericarps are very different. *Malvastrum guatemalense* is not only geographically isolated from *M. bicuspidatum,* but its occurrence in mesic, forested regions rather than in semi-arid areas suggests that it is also ecologically (or physiologicaly) isolated from the latter species.

SPECIMENS EXAMINED. **Guatemala.** SANTA ROSA: near Cuilapa, *Standley 77661* (F); near Cuilapa, *Standley 78534* (F); **Honduras.** CHOLUTECA: Bella Vista, *Williams & Molina 10865* (F); **Nicaragua.** MATAGALPA: 5–10 km W of Matagalpa, *Williams et al. 23821* (G, NY, TEX, US).

9a. **Malvastrum bicuspidatum** (S. Watson) Rose subsp. **bicuspidatum,** Contr. U. S. Natl. Herb. **12**: 286. 1909. Fig. 45, 46.

Malvastrum tricuspidatum (R. Br. in Aiton) A. Gray var. *bicuspidatum* S. Watson, Proc. Amer. Acad. Arts **21**: 417. 1886. TYPE: MEXICO. Chihuahua, Hacienda San Miguel, 1 mile from Batopilas along the Batopilas River, alt. 2400 feet, August, 1885. *E. Palmer 8* (HOLOTYPE: GH! ISOTYPES: BM!, K!, MICH!, NY!, PH!, US!).

Sphaeralcea scoparia sensu Tidestrom, Proc. Biol. Soc. Wash. **48**: 41. 1935, excl. basionym. Applied to specimens of *M. bicuspidatum* from Arizona.

Suffruticose perennial herb to 1.5 m tall but occasionally dwarfed to 0.4 m, typically rather sparsely branched (bushy-branched in the Tucson Mountains); *stems* 4–8 mm diam at base; *branches* 25–50 cm long; *vesture* of appressed (4) 5-rayed stellate hairs 1 mm diam directed longitudinally on the stem and minute 4–8-rayed stellate hairs 0.3 mm diam, shed in age; *cotyledons* ovate to broadly elliptic, rounded at the apex, widely cuneate at the base, 9.0–9.5 mm long × 8.5 mm wide, petiole 7–8 mm long; *stipules* (3) 5–6 (8) mm long × 1 mm wide, somewhat falcate, narrowly lanceolate; *petioles* (6) 10–25 (70) mm long; *blades* (1.8) 2.5–3.5 (4)× longer than the petioles, (13) 30–50 (100) mm long × (11) 15–30 (90) mm wide, average midstem blade 1.3–1.7× longer than wide, earliest vegetative blades wide-ovate to obscurely 3-lobed often as wide as long and broader than

those produced later on upper portions of the stem, mid- and upper stem blades narrowly ovate to nearly lanceolate, unlobed, base of youngest blades obscurely cordate to truncate and rounded to wide-cuneate in upper leaves, apex acute to acuminate, margin dentate to sharply dentate with 3–5 teeth cm, vesture of the adaxial surface a mixture of fine-textured predominately 4-rayed stellate hairs and simple to 5–8-rayed hairs 1.0 mm diam, abaxial vesture similar but simple hairs scarce or absent; *flowers* typically solitary in the axils of upper leaves and stipules at first, later borne in elongated racemes at branch apices in axils of bifid bracts, occasionally produced in highly reduced few-flowered racemes in upper leaf axils associated with primary inflorescence; *floral bracts* divided 1/4 to 1/2 their length; *pedicels* normally 0.5 1.5 (5) mm long appearing longer in flowers produced on leafless single-flowered articulated axillary branches at the base of the inflorescence, increasing by 0.5–1.0 mm in fruit; *involucel* of 3 narrowly lanceolate to lanceolate somewhat falcate bracteoles 4–6 mm long × 0.5–1 mm wide, spirally inserted on the calyx at different levels, united to the calyx 1–2 mm below; *calyx* united 1/4 to 1/2 its length, 6–8 mm from pedicel to apex of lobes to 7–9 mm in fruit, rotate, lobes patent, deltate to triangular, acute to acuminate-cuspidate, in fruit 5–7 mm long × 3–4 mm wide, vesture of sparse stellate 2 6-rayed hairs and a few simple marginal hairs 0.8 1.5 mm diam but the lobes not especially ciliate, and with frequent minute stellate 5–8-rayed hairs 0.2–0.4 mm diam, base of calyx with surface obscured, lobes downy-pubescent in upper 2 3 within with minute arachnoid simple hairs; *corolla* orange to orange-yellow, petals slightly asymmetric but lobes subequal, petals 6–8 mm long × 7 mm wide, rotate, exceeding the calyx 3–4 mm, claw pubescent at base with dense stellate hairs; *androecium* with (30) 36 45 (58) stamens tending towards 40, filament tube 2 3 mm long pubescent with sparse spreading 2 5-radiate stellate hairs, free portion of filaments 0.9 1.0 mm long; *gynoecium* with 9–12 carpels, style branching 2 mm above the columella, each branch terminated by an expanded hemispherical to subglobose stigma exceeding the stamens by 1–1.5 mm recurved at flower wilt; *schizocarps* (5.5) 6–7 (8) mm diam including ornamentation *mericarps* 9 12, 1.8 2.0 mm in height × 3–4 mm in length × 1 mm in width including ornamentation, often tinted pale rose before drying tan, lacking a proximal cusp or with a small mucro less than 0.1 mm long, with

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two conspicuous divergent distal-apical cusps (0.5) 1.0–1.5 mm long, lateral faces conspicuously ribbed, distal and apical surfaces with an inconspicuous raised medial line obscured by hairs, vesture of the distal and apical surface and cusps consisting of rigid simple hairs 0.1–1.0 mm long mixed with smaller simple stellate and intermediate hairs, the lateral faces essentially glabrous except on the extreme margins and near the cusps, pericarp firm and woody, completely indehiscent, endoglossum lacking; *seeds* 1.5 mm in height × 2 mm in length × 0.8 mm wide, furrowed on the distal-apical surface; *chromosome number:* $n = 12$, $2n = 24$; *pollen* 51–67 (60) μm, echinae 3.8–4.0 μm, apertures 5 to 7, usually 7.

DISTRIBUTION. (Fig. 44). Known from slopes in arid and semi-arid regions of low to moderate elevation, 30 1300 m, primarily in the Sonoran Desert: from the Tucson Mountains of Arizona in the north, to southern Sinaloa in the south, to northeastern Sonora and extreme southwestern Chihuahua in the east, and west nearly to the coast with an outlying station in south-central Baja California.

PHENOLOGY AND REPRODUCTIVE BIOLOGY. Flowering in late August to mid-October in the north and into late November towards the south, sparingly into January and February. In the Arizona population flowering occurs again in late March to early May on new growth after winter rains, but ceases again until late summer rains fall. This pattern was repeated in plants grown from seeds (as much as 24 years old) in Texas at nearly the same latitude. The first flowers were produced after 120 days growth, and were

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Figure 45. *Malvastrum bicuspidatum* subsp. *bicuspidatum*. a. Habit, scale = 5 cm. b. Flower-bud and bract, scale = 2 mm c. Petal, scale = 2 mm. d. Stamens, styles, and stigmas, scale = 2 mm. e. Floral bract, scale = 2 mm. f.–h. Mericarp, lateral, distal, and apical views, scale = 1 mm. i. Mericarp, internal view, scale = 1 mm. j. Fruit, apical view, scale = 2 mm. k. Seed, scale = 1 mm. l. Fruiting calyx, lateral-basal view, scale = 2 mm. m. Columella and carpocrater, scale = 0.5 mm. n. Stipule, scale = 2 mm. o. Bracteole, adnate portion stippled, scale = 2 mm. p. Leaf, from inflorescence base, scale = 2 cm. q. Leaf, early vegetative growth, scale = 2 cm. r. Cotyledon, scale = 5 mm. s. Stem vesture, scale = 0.5 mm. t. Vesture, adaxial leaf surface, scale = 0.5 mm. u. Vesture, mericarp, scale = 0.5 mm. (a,e,k–m, o from progeny of *Bye 6940;* b from *Shreve 6111;* c–d,p,s u from *Palmer 8;* f–j, n from *Palmer 790;* q from *Fryxell 3082;* r from progeny of *Lehto, et al. 19487*).

MEXICAN FLORA
HOLOTYPE of Malvastrum tricuspidatum (Alt.) A.Gray var. bicuspidatum S. Watson, Proc. Amer.Acad Arts 21:417, 1886
Determined by Steven R. Hill

then produced continually for five months. The plants were dormant during the winter. The flowers generally opened in the mid or late afternoon (2:30 CST) and remained open until after sunset (until 7:30 CST) occasionally remaining open all night and closing the next day. The stigmas are at first well-exserted from the stamen column but, as the flower wilts, they bend back and self-pollinate. Emasculated flowers do not set fruit. Outcrossing seems to be encouraged by the exserted stigmas that remain exserted for nearly five hours, but fruit is insured by an effective system for self-pollination. Fruits mature in 23–29 days after anthesis.

DISCUSSION. *Malvastrum bicuspidatum* subsp. *bicuspidatum* is the northernmost taxon of the section *Tomentosum,* and is readily distinguished by its long-cuspidate, strongly ribbed mericarps, and its unique vesture patterns. Several authors have treated the species as a northern population of *M. tomentosum* (as *M. scabrum*, etc.) since the mericarps are superficially very similar. However, all of the Central American members of the section have lanceolate rather than linear-filiform bracteoles.

Individuals of the typical subspecies growing at the periphery of its range usually are more compact xerophytes. Plants grown with an abundance of water have larger leaves, and flower for longer periods with more elongated racemes. Individuals from Arizona most resemble individuals of *M. tomentosum* in South America in vesture characters of the leaves and mericarps and may represent an early "invasion-form", but the plants have all of the diagnostic characters more typical of *M. bicuspidatum.*

REPRESENTATIVE SPECIMENS: **United States.** ARIZONA: Pima Co., Sierra Tucson, *Pringle 10787* (BR, F, G, GH, MICH, MO, NY, PENN, US, VT); Pinal Co., Devil's Canyon, near Superior, *Harrison 3094* (US). **Mexico.** SONORA: Agiabampo, *Palmer 790* (K, US); 12 mi. S of Ortiz, *Shreve 6111* (F); 16 mi. S of Hermosillo on road to La Palma, *Wiggins & Rollins 206* (DS, GH, MICH, MO, NY, TEX, UC, US); 4 mi E of Willard, between Hermosillo and Sahuaripa, *Wiggins & Rollins 290* (DS, GH, MICH, MO, NY, TEX, UC, US); Sierra Bojihuacame, SE of Cd. Obregon, steep slope, *Gentry 14522* (TEX, US); 14 mi. E of Navojoa, *Lehto et al. 19487* (pf); 19 mi S of Magdalena on road to Cucurpé, *Fryxell 3082* (pf); CHIHUAHUA: Arroyo La Bufa above río Batopilas, *Bye 6940* (pf); SINALOA: Culiacán, *Brandegee s n.* (GH, POM, UC, US); Maraton, 12 mi W of Culiaćan, *Gentry 7015* (DS, GH); BAJA CALIFORNIA: Comondú, *Brandegee s.n.* (F, PH, UC, US): San Bernardo Cañon, *Brandegee s.n.* (UC).

Figure 46. *Malvastrum bicuspidatum* subsp. *bicuspidatum* (holotype).

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9b. **Malvastrum bicuspidatum** (S. Watson) Rose subsp. **campanulatum** S. R. Hill, Brittonia **32**(4): 470. 1980. Fig. 47, 48.
TYPE: MEXICO. Hidalgo: near Tepejí del Río, alt. 7500 ft, on brushy hillside, 28 Oct 1972, *P. A. Fryxell & D. M. Bates 2175* (HOLOTYPE: BH!; ISOTYPES: CAS!, CTES, ENCB, pf!).

Suffruticose perennial (1.0) 1.5 (2.0) m tall, usually few-branched in the first year; *vesture* of all parts more dense than in subsp. *bicuspidatum,* stem with stellate hairs 0.3–2 mm diam with 6–8 rays; *cotyledons* wide-ovate, 9 mm in length × 10 mm in width, briefly emarginate at the apex, truncate or broadly rounded at the base, petiole ca. 4 mm long; *blades* 5–6× longer than the petioles, ovate to narrowly ovate, rarely minutely 3-lobed 1/3 the distance from the base, vesture of the adaxial surface generally of 5–6-rayed stellate hairs, only infrequently with 1–4- or more than 6 rays; *flowers* in few densely compacted racemes, often only one raceme the first year, 2–3-flowered axillary racemes generally lacking or few; *floral bracts* in the upper portions of the raceme deeply divided 1/2–2/3 to the base or with 3-lobed transitional forms, densely pubescent; *pedicels* not exceeding 1.5 mm, scarcely increasing in fruit; *involucel* bracteoles lanceolate, 5–7 mm long × 1.0–1.3 mm wide and densely pubescent, appearing ciliate; *calyx* lobed halfway to base, 9–10 mm from pedicel to lobe apex, shape in profile campanulate, lobes spreading to a lesser degree than in subsp. *bicuspidatum,* entire calyx densely pubescent with the outside surface obscured, margins of lobes ciliate; *petals* 10–12 mm long × 9 mm wide, darker orange than in subsp. *bicuspidatum* in cultivated plants; *androecium* with (49) 60–75 stamens (nearly 2× that of other subsp.); *gynoecium* with (10) 12 (13) carpels, terminal subhemispherical stigmas exserted from the anthers by less than 1.0 mm, not expanded; *schizocarps*

Figure 47. *Malvastrum bicuspidatum* subsp. *campanulatum*. a. Habit, scale = 5 cm. b. Stamens, styles and stigmas, scale = 2 mm. c. Vesture of adaxial leaf surface, scale = 0.5 mm. d. Mericarp vesture, scale = 0.5 mm. e–g. Mericarp, lateral, distal and apical views, scale = 1 mm. h. Mericarp internal surface, scale = 1 mm. i. Fruit, apical surface, scale = 2 mm. j. Seed, lateral and apical views, scale = 1 mm. k. Calyx in fruit, profile, vesture excluded, scale = 1 mm. l. Columella and carpocrater, scale = 0.5 mm. m. Floral bracts, transitional above, fully developed below, scale = 2 mm. n. Stipule, scale = 2 mm. o. Bracteole, adnate portion stippled, scale = 2 mm. p. Leaf variation, mid-stem and apical leaves, scale = 2 cm. q. Cotyledon, scale = 5 mm. (a–h, j–l, n and q from progeny of *Waterfall & Wallis 13918,* i. m and o–p from *Fryxell, et al. 1624*).

7 8 mm diam; *mericarps* (10) 12 (13), 2.0 mm in height × 3.0 mm in length ×1.2 mm wide, with two distal-apical cusps (0.1) 0.5 (0.8) mm long, lateral faces only slightly ribbed, vesture similar to that of subsp. *bicuspidatum* but often with few simple hairs and generally shorter stellate hairs giving the surface a fine-canescent appearance, mericarp texture woody, endoglossum lacking; *seeds* with inconspicuous distal-apical sulcus; *chromosome number*: $n = 12$, $2n = 24$; *pollen* 53–79.4 (60) μm, echinae 3.8–5 μm, apertures 6–9.

DISTRIBUTION. (Fig. 44). Restricted to the semi-arid Mexican central high plateau (altiplanicies central), from eastern Jalisco in the west to southwestern Hidalgo in the east at elevations of 1200 2500 m.

PHENOLOGY AND REPRODUCTIVE BIOLOGY. Flowering primarily in mid-August to November, but may bloom after rains into January and again in June. In cultivation (seeds from *Waterfall & Wallis 13918*) the flowers opened at least one hour after those of the typical subspecies (4 4:30 pm CST) and closed after sunset (7:30 pm CST), occasionally remaining open until the next morning. In cooler periods, a few flowers opened in the morning, 9:30 CST and closed at the usual time. Self-pollination may be common in native populations due to the close proximity of the anthers with the stigmas.

DISCUSSION. Especially diagnostic for this subspecies are the floral characters (e.g. numerous stamens, subequal styles, unex-panded stigmas), the derived mericarp features (such as the reduced cusps and ribbing), the vesture features, and the pronounced campanulate calyx. The latter feature, very conspicuous in living plants, was used as the basis of the subspecies epithet. It is thought that the reductional features and the nearly obligate autogamous reproduction are derived from the ancestral state seen in subsp. *bicuspidatum*.

SPECIMENS EXAMINED: **Mexico.** JALISCO: rocky hillside above lake Chapala near Tuxcueca, *Leavenworth & Leavenworth 1910* (F); GUANAJUATO: near Guanajuato, *Kenoyer 1744* (A); 59 mi. SE of Salamanca, *Waterfall & Wallis 13918* (F, SMU); QUERÉTARO: Palobobo valley NW of Querétaro, *Gregg 594* (GH, MO, NY); Querétaro, *Berlandier 1290* (GH); 10 km. N of Querétaro, *Flores-Crespo 346* (ENCB,

Figure 48. *Malvastrum bicuspidatum* subsp. *campanulatum* (isotype, pf).

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Cotton Branch Herbarium

MICH, pf); 7 mi. N of Querétaro, *Fryxell 770* (BH, CTES, MEXU, pf, SASK, UC, US); Hwy. 57, N of Querétaro across from Pemex Station, *Dunn & Dunn 18480* (MO, pf); HIDALGO: near Tepejí del Río, *Fryxell & Bates 2175* (BH, CAS, pf); MICHOACÁN: 15 mi. E of Jiquilpan, *Fryxell et al. 1624* (BH, pf); Monte León, *Pringle 13851* (collected Lozano) (CAS, GH, MICH, SMU, US, VT).

9c. **Malvastrum bicuspidatum** (S. Watson) Rose subsp. **oaxacanum** S. R. Hill, Brittonia, **32**(4): 478. 1980. TYPE: MEXICO. Oaxaca: Monte Albán, Oaxaca City, 5 Sep 1894, *C. G. Pringle 5778* (HOLOTYPE: VT!; ISOTYPES: C!, GH!, US!) Fig. 49, 50.

Malvastrum oaxacanum Rose ex Davis, Life and Work of C. G. Pringle: 405. 1936, nomen nudum. A manuscript name.

Sparsely branched compact suffruticose perennial, stem hairs somewhat tuberculate; *leaf blades* 25 40 mm long × 15 20 mm wide, ovate-lanceolate, occasionally briefly 3-lobed 1 3 the distance from the base, vesture of the adaxial surface of stellate (2) 5 6-rayed hairs and simple hairs in the Puebla population and of simple or 2-rayed hairs in the Oaxaca population, the vesture of the abaxial surface dense with 10 12-rayed stellate hairs, leaves paler beneath; *flowers* in congested terminal racemes, solitary-axillary in leaf axils at first and not infrequently in several reduced racemes from upper leaf axils; *calyx* conspicuously ciliate; *petals* 10 14 mm long × 8 10 mm wide; *stigmas* exserted from the anther cluster by 2 mm; *mericarp* similar to that of subsp. *tumidum* in its leathery texture, but with a firm proximal-apical endoglossum on the internal surface, external surface at apex pubescent with small stellate hairs 0.5 mm or less long, pericarp surfaces smooth except for ribs at the distal-lateral margins giving margins a crenate appearance in profile, raised midline present on distal-apical surface, *seeds* symmetrically reniform, without a sulcus; *chromosome number:* $2n = 24$; *pollen* 59 79.4 (68.7) μm diam, echinae 2.6 3.8 μm, apertures 6–9 (usually 7).

Figure 49. *Malvastrum bicuspidatum* subsp. *oaxacanum*. a. Habit, scale = 5 cm. b. Stamens, styles and stigmas, scale = 2 mm. c–e. Mericarp, lateral, distal and apical views, scale = 1 mm. f. Mericarp, internal view, scale = 1 mm. g. Fruit, apical view, scale = 2 mm. h. Seed, scale = 1 mm. i. Calyx, early fruit, scale = 2 mm. j. Columella and carpocrater, scale = 0.5 mm. k. Floral bract, scale = 2 mm. l. Stipule, scale = 2 mm. m. Bracteole, scale = 2 mm. n. Leaf, scale = 2 cm. o. Adaxial leaf vesture, scale = 0.5 mm. p. Stem vesture, scale = 0.5 mm. (a,c–e, g, j m and p from *Smith 644;* b, i and n–o from *Pringle 5778*; f and h from *Krapovickas & Cristóbal 23596*.)

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DISTRIBUTION. (Fig. 44). Known only from Coxcatlan, Puebla and Monte Albán, Oaxaca on semi-arid slopes at an altitude of 1800 2600 m and is probably to be found at suitable sites in between.

PHENOLOGY AND REPRODUCTIVE BIOLOGY. According to specimen labels, plants were in flower from early September to early November and in fruit into January. Daily flowering periods are not known. The exserted stigmas suggest effective cross-pollination, but the populations may be small and inbred.

DISCUSSION. *Malvastrum bicuspidatum* subsp. *oaxacanum* grows in some of the most arid portions of the range of the species. In such regions its thick indument might aid in water conservation. The presence of an endoglossum and absence of simple hairs on the mericarp readily distinguish this subspecies from the others in *M. bicuspidatum*. The texture of the pericarp and the mature inflorescence habit ally it with subsp. *tumidum*. The endoglossum is probably retained here by chance and again demonstrates the affinity of *M. bicuspidatum* with *M. tomentosum*. I have chosen Rose's invalid but appropriate specific epithet as the basis of the subspecific epithet.

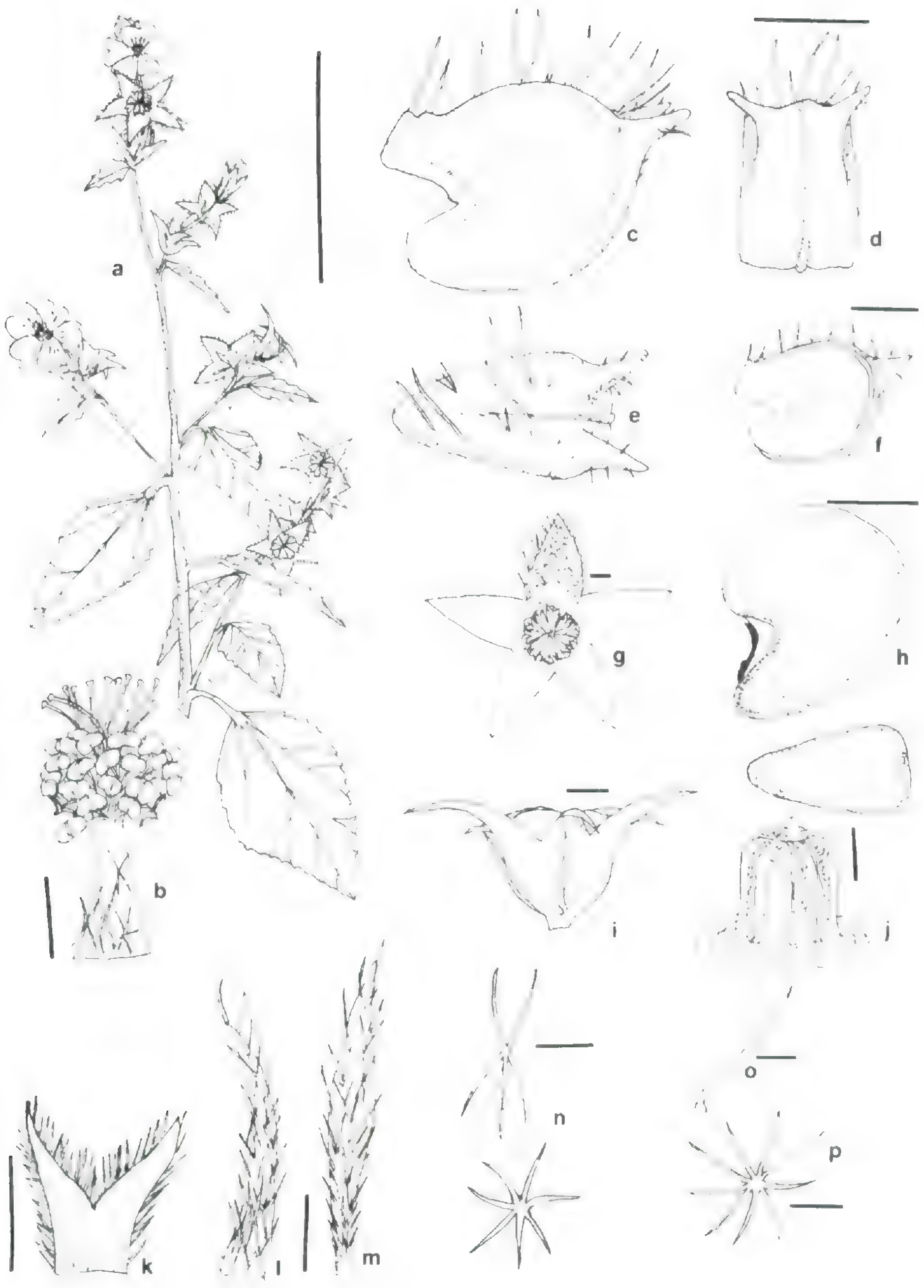
SPECIMENS EXAMINED: **Mexico.** PUEBLA, Coxcatlan, *Purpus 4185* (GH, NY, UC, US); OAXACA: Monte Albán, *Smith 644* (CAS, F, MO, NY, RSA, UC, US); Monte Albán, *Krapovickas & Cristóbal 23596* (pf); Monte Albán, *Krapovickas 8215* (G).

9d. **Malvastrum bicuspidatum** (S. Watson) Rose subsp. **tumidum** S. R. Hill, var. **tumidum,** Brittonia **32**(4): 474. 1980. TYPE: MEXICO. Jalisco: Valley of Tequila, 27 Sept 1893, *C. G. Pringle 5452* (HOLOTYPE: VT!; ISOTYPES: F!, GH!, MICH!, MO!, US!). Fig. 51, 52.

Suffrutescent perennial 1.0 -2.0 m tall, frequently branching in the upper third; *stem and branches* as in subsp. *campanulatum,* branches apparently short; *cotyledons* not known; *blades* tending to be ovate-elliptic, with an adaxial vesture of fine simple hairs l 1.5 mm long imparting to the leaf a felty texture, the few stellate hairs restricted to the base on lower veins or to apical leaves, abaxial

Figure 50. *Malvastrum bicuspidatum* subsp. *oaxacanum* (holotype).

C. G. PRINGLE.
PLANTÆ MEXICANÆ
5778 STATE OF HIDALGO
Malvastrum oaxacanum,
Monte Alban, Oaxaca,
5 Sept., 1894.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vesture loose, of 5–8-rayed hairs; *flowers* borne on several reduced floriferous branches in the axils of upper leaves even in young plants, the leafless portion of the raceme less than 10 cm long, the flowers somewhat congested; *floral bracts* lobed halfway to the base, 2.5 mm long × 2.5 mm wide; *pedicels* 1–3 mm, scarcely increasing in fruit; *involucel* as in the typical subspecies but strigose-pubescent with a ciliate margin; *calyx* divided 1/2 to 2/3 to the base, with a somewhat campanulate base and slightly spreading lobes, external surface varying from sparsely to densely pubescent, the margins of lobes conspicuously ciliate with simple hairs 1–1.5 mm long in contrast to the typical subspecies; *petals* 7–10 mm long × 8 mm wide; *androecium* with 38–49 stamens, tending towards 40; *gynoecium* with 10–11 carpels, stigmas expanded hemispherical, exserted 1–2 mm above the anther cluster; *schizocarps* 6 8 mm diam; *mericarps* 10–11, often tinted rose drying to red-brown or brown, 2.0 mm in height × 3.0 mm in length × 1.0–1.5 mm in width appearing swollen, with 2 apical-distal cusps 0.8 0.9 mm long, lateral faces unribbed, somewhat shiny, apical-distal surface with a conspicuous raised medial line, vesture consisting of a few fine simple or 2–3-rayed hairs 0.5 1.0 mm long or with a few minute 2–5 rayed stellate hairs 0.2 mm diam, restricted to the apical and cusp surfaces, lateral and distal surfaces glabrous, pericarp flexible leathery or chitinous, endoglossum lacking; *seeds* 1.5 2 mm long × 2 mm in height × 0.8 mm in width with a very inconspicuous distal-apical sulcus or this absent; *chromosome number:* not known; *pollen* 66.6 79.4 (74.5) μm diam, echinae 3–5 μm, apertures 6–9.

DISTRIBUTION. (Fig. 44) Restricted to the transverse volcanic belt of Mexico between 1200 1900 m elevation, from Jalisco to Michoacan and Morelos.

Figure 51. *Malvastrum bicuspidatum* subsp. *tumidum* var. *tumidum*. a. habit, scale = 5 cm. b. Stamens, styles and stigmas, scale = 2 mm. c e. Mericarp, lateral, distal and apical views, scale = 1 mm. f. Mericarp, internal view, scale = 1 mm. g. Fruit, apical view, including vesture of single lobe, scale = 2 mm. h. Seed, lateral and apical views, scale = 1 mm. i. Fruiting calyx profile, excluding vesture, scale = 2 mm. j. Columella and carpocrater, scale = 0.5 mm. k. Floral bract, scale = 2 mm. l. Stipule, scale = 2 mm. m. Bracteole, scale = 2 mm. n. Stem vesture, scale = 5 mm. o. Adaxial leaf vesture, scale = 0.5 mm. p. Abaxial leaf vesture, scale = 0.5 mm. (a,c–e and g p from *Fryxell & Bates 2143*; b and f from *Pringle 5452*.)

Figure 52. *Malvastrum bicuspidatum*[1] subsp. *tumidum* var. *tumidum* (holotype).

PHENOLOGY AND REPRODUCTIVE BIOLOGY. Flowering primarily in September to November. Daily flowering time not known.

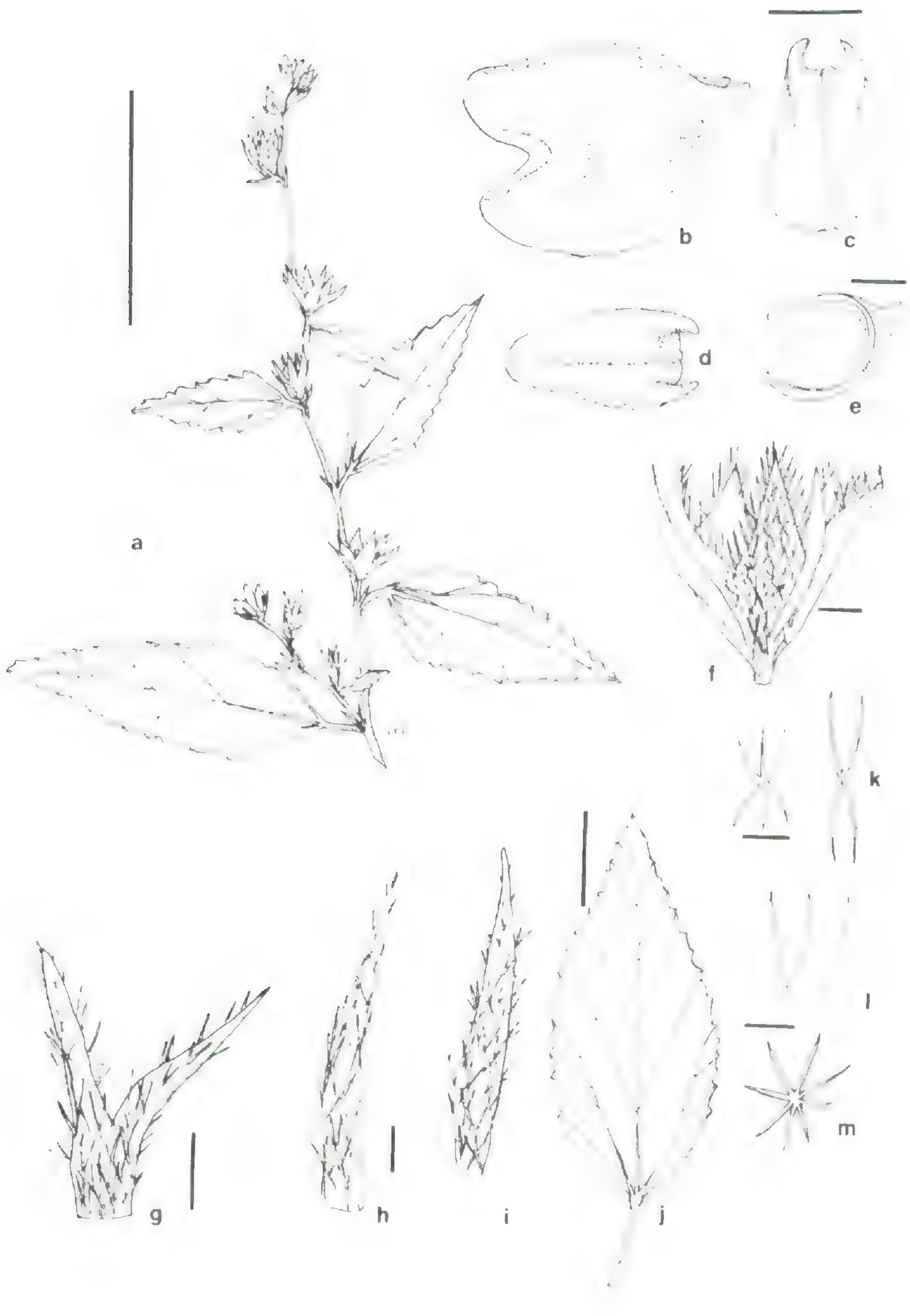
DISCUSSION. The leathery nearly glabrous swollen and often rose-tinted mericarps of *Malvastrum bicuspidatum* subsp. *tumidum* are its primary diagnostic features. Vegetative and inflorescence characters closely resemble the corresponding characters in *M. guatemalense,* but the mericarps are very different. *Malvastrum bicuspidatum* subsp. *tumidum* is the most mesophytic of the subspecies as reflected in the larger wider leaves and generally sparse vesture on vegetative parts. It is apparently well-adapted to the fertile soils of the volcanic belt in regions with moderate rainfall. It is suspected that seeds of this subspecies are dispersed by birds, a change from the probable ancestral mammalian dispersal mode; this conclusion is based on the reduction of transport mechanisms and pericarp strengthening features (such as the ribs), and on the rose-red color of the young mericarps.

SPECIMENS EXAMINED: **Mexico.** JALISCO: Valley of Tequila, *Pringle 5452* (F, GH, MICH, MO, US, VT); 15 km. W. of Ayutla towards Cuautla, *Fryxell & Bates 2143* (BH, MEXU, MICH, pf); 2 mi S of Jocotepec on Route 15, *Harker & Mellowes 33* (BM); Ixtlahuacan de los Membrillos, *Detling 8753* (MICH); MICHOACAN: mountain above Lake Chapala near KM 543, 8 mi NW of Sahuayo, *McVaugh 18147* (MICH, US); MORELOS: Iturbide, Cuernavaca, *Bourgeau 1170* (GH); near Cuernavaca, *Rose & Hough 10246* (GH, US).

9e. **Malvastrum bicuspidatum** (S. Watson) Rose subsp. **tumidum** S.R. Hill var. **glabrum** S. R. Hill, Brittonia **32**(4):476. 1980. TYPE: MEXICO: Michoacan: Between Tuxpan and Ciudad Hidalgo, 3 miles north of Tuxpan, alt. 5700 ft, October 14, 1970. *P. A. Fryxell, D. M. Bates & O. Blanchard 1642* (HOLOTYPE: BH!; ISOTYPES: CTES, ENCB, pf!). Fig. 53, 54.

Very similar to the typical variety of subsp. *tumidum* but differing in its more narrowly ovate-lanceolate leaves, (some of which are 8 times longer than the petioles), in the erect calyx lobes in fruit, and in its smaller glabrous schizocarps ca. 5.0 mm in diameter that are bright red apically when mature, the color fading slightly upon drying; *chromosome number:* not known; *pollen:* 71.7 79.4 (75.9) μm diam, echinae 3.8 μ m, apertures 7–8.

DISTRIBUTION. (Fig. 44) Known only from the type locality 3 miles north of Tuxpan, Michoacan, Mexico.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PHENOLOGY AND REPRODUCTIVE BIOLOGY. The type specimen was in flower and with young fruit when collected in mid-October; daily flowering period not known.

DISCUSSION. Glabrous mericarps are found in no other species of *Malvastrum*, and so this new variety is considered to be noteworthy. It occurs at a point of contact between the ranges of *M. bicuspidatum* subsp. *campanulatum* and *M. bicuspidatum* subsp. *tumidum* var. *tumidum*, but has no hybrid characters.

SPECIMENS EXAMINED. **Mexico.** MICHOACAN: between Tuxpan and Ciudad Hidalgo, 3 mi north of Tuxpan, alt. 5700 ft, *Fryxell et al. 1642* (BH, pf).

Section 5. *Amblyphyllum*

Malvastrum sectio **Amblyphyllum** S. R. Hill, *sect. nov.*

Carpella matura 11–18, indehiscentia, superficie apicali pilis simplicibus, muris lateralibus pericarpii crassis et costatis, cuspidibus 2 distali-apicalibus 0.5–1.5 mm longis et cuspide unico proximali-apicali 0.1–1.0 mm longo ornata, marginibus pericarpii distalibus alatis, endoglosso nullo; stamina 26 111, columna staminali pubescenti; flores solitarii axillares ad apicem conferti; bracteolae involucelli basi ad calycem adnatae vel liberae; bracteae florales bifidae nullae; pili caulini nunquam stipitati; pollinis grana aperturis 15–35. Typus: *Malvastrum amblyphyllum* R. E. Fries

The solitary axillary flowers, indehiscent, thick-walled elaborately ribbed and marginally winged mericarps, lack of an endoglossum and bifid floral bracts, pubescent filament tube, and 15 35 aperturate pollen characterize the section *Amblyphyllum*.

10. **Malvastrum grandiflorum** A. Krapovickas, Bol. Soc. Argent. Bot. **15** (4): 467, f. 1. 1974. TYPE: BOLIVIA. Tarija: Ysyry, 40 km.

Figure 53. *Malvastrum bicuspidatum* subsp. *tumidum* var. *glabrum*. a. Habit, scale = 5 cm. b d. Mericarp, lateral, distal and apical views, scale = 1 mm. e. Mericarp, internal view, scale = 1 mm. f. Calyx in fruit, vesture of one lobe only, scale = 2 mm. g. Floral bract, abaxial surface, scale = 2 mm. h. Stipule, abaxial surface, scale = 2 mm. i. Bracteole, abaxial surface, scale = 2 mm. j. Leaf, scale = 2 cm. k. Stem vesture, scale = 0.5 mm. l. Leaf adaxial surface vesture, scale = 0.5 mm. m. Leaf abaxial leaf surface vesture, scale = 0.5 mm. (All from *Fryxell et al. 1642*.)

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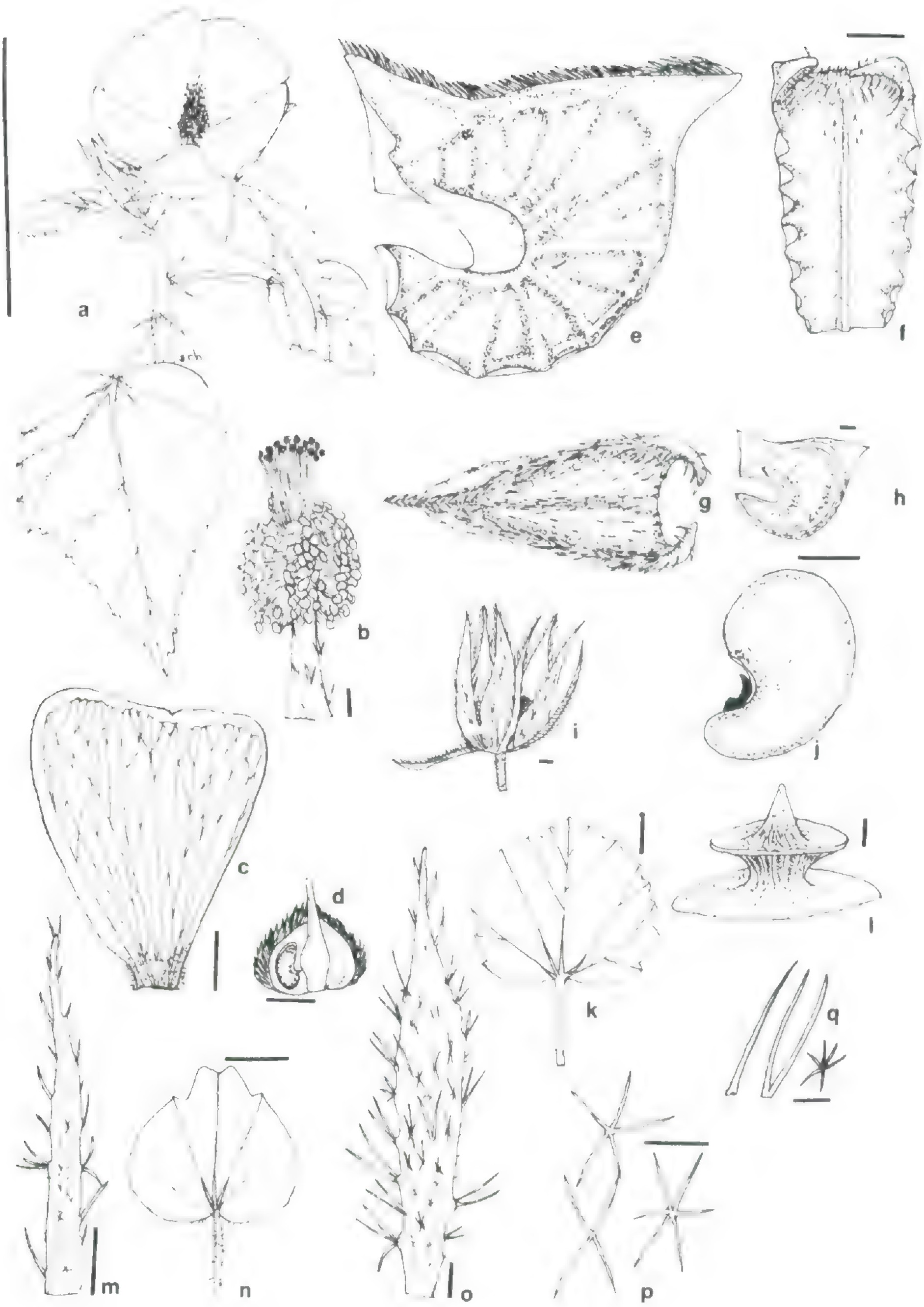
Cotton Branch Herbarium
Collector
Date
No.

W of Villa Montes on road to Tarija, altitude 500 meters, May 26, 1971. *A. Krapovickas, L. A. Mroginski,* and *A. Fernández 19300* (HOLOTYPE: CTES; ISOTYPES: BA, BAA, BAB, BH!, G!, GH!, K!, LIL, LP, NY!, P, pf!, SI, UC, US!) Fig. 55, 56.

Suffruticose sparsely branched *perennial* herb 1.7 m tall; main *stem* 4–8 mm diam at base, with primary *branches* 20 60 cm long *vesture* of appressed non-persistent (4) 5–6 (7)-rayed stellate hairs 0.6 1.0 mm diam slightly overlapping on young branches and sparse on older branches; *cotyledons* 9 mm long × 11 mm wide, wide-ovate, 3-lobed, emarginate at the apex and slightly cordate at base, palmately 5-nerved; *stipules* (7) 10–16 mm long × 1.0–1.5 mm wide, narrowly-lanceolate, subfalcate, long-acuminate; *petioles* (5) 20 50 (60) mm long; *blades* 1.6–2.6× longer than the petioles, ovate, unlobed to obscurely 3-lobed 1/2 to 2/3 the distance above the base, base slightly cordate broadly rounded to somewhat truncate, apex acute to acuminate, seedling leaves sub-orbicular or sometimes wider than long with a cordate base and rounded apex, blades (30) 70 90 (130) mm long × (20) 50 70 (85) mm wide, average midstem blade 1.3 1.5× longer than wide, margins dentate to sharply dentate with 1.5–3 teeth/cm, vesture of the adaxial surface of evenly scattered (5) 6 (8)-rayed stellate hairs 0.3–1.0 mm diam with a few enlarged apically or marginally directed rays, abaxial vesture dense with similar 8–10-rayed hairs not obscuring the leaf epidermis; *flowers* solitary-axillary, later aggregated in terminal spicate racemes subtended by reduced leaves and their stipules, the congested appearance owing to shortening of the internodes; *pedicels* 2–4 mm long increasing 1 mm or less in fruit; *involucel* of 3 lanceolate to narrowly lanceolate, subfalcate bracteoles (15) 17 18 mm long × 2.5–3.0 mm wide, free from the calyx or slightly adnate in basal 1.0 mm; *calyx* united 1/5 to 1/3 its length, 15 mm from pedicel to apex in flower and 20 mm in fruit, slightly accrescent, broadly campanulate at anthesis and narrowly campanulate in fruit, lobes slightly spreading in flower and erect in fruit, narrowly triangular, acuminate, 12–15 mm long × 5–6 mm wide, somewhat tomentose on the outside with sparse simple or 2-rayed hairs 2 mm long directed apically and dense 4–8-rayed stellate hairs 0.5 mm

Figure 54. *Malvastrum bicuspidatum* subsp. *tumidum* var. *glabrum* (isotype, pf).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diam usually obscuring the surface, lobes pubescent within on upper 2/3 with sparse minute simple hairs; *corolla* to 47 mm diam when spread, golden-yellow to yellow-orange, petals slightly asymmetrically bilobed, 17–23 mm long × (12) 15 mm wide, widespread at anthesis, exceeding the calyx by 4–5 mm, claws red, slightly pubescent marginally with fine simple hairs 0.5 mm long; *androecium* with 108–111 stamens in 5 longitudinal rows, filament tube 6 7 mm long, sparsely pubescent with minute 2 4-rayed hairs, free portion of filaments 1.5–2.0 mm long, anthers 1.3–1.5 mm long × 0.8 mm wide after dehiscence; *gynoecium* with (13) 16 18 loosely coherent carpels, style branching 8 mm above the columella, each branch terminated by an enlarged hemispherical magenta stigma conspicuously raised above the anthers by 3 5 mm, ovary surface densely pubescent with simple ascending centrally directed hairs; *schizocarps* 8 mm diam including ornamentation; *mericarps* (13) 16–18, 3.0–3.5 mm in height × 4–5 mm in length including ornamentation × 2.0 mm in width, usually with a fragile flattened proximal-apical cusp 1.0 mm long and two flattened distal-apical cusps 1.0 1.5 mm long the latter distinctly separate but curved towards one another, lateral faces with conspicuous opaque ribs extending into a thin translucent slightly winged border extending 0.1–0.3 mm from the mericarp body, distal surface with a conspicuous raised medial line, vesture on the apical surface primarily of strigose coarse rigid proximally directed simple hairs 0.5 0.7 mm long with a few simple downy hairs on the central portion of the lateral faces and near the apex of the distal surface, pericarp woody and indehiscent, the proximal-apical region thin and solid, endoglossum lacking, tardily deciduous from the receptacle at maturity due to the enclosing calyx lobes; *seeds* narrower in the basal half below the hilum, 2.5 mm in height × 2.0

Figure 55. *Malvastrum grandiflorum*. a. Habit, scale = 5 cm. b. Stamens, style, and stigmas, scale = 2 mm. c. Petal, scale = 5 mm. d. Ovary at anthesis, carpel dissected to show ovule, scale = 1 mm. e. g. Mericarp, lateral, distal, and apical views, scale = 1 mm. h. Mericarp, internal view, scale = 1 mm. i. Calyx in fruit, scale = 2 mm. j. Seed, scale = 1 mm. k. Seedling leaf, scale = 1 cm. l. Columella and carpocrater, scale = 0.5 mm. m. Stipule, scale = 2 mm. n. Cotyledon, scale = 5 mm. o. Bracteole, scale = 2 mm. p. Stem vesture, scale = 0.5 mm. q. Calyx vesture, scale = 0.5 mm. (All drawn from cultiv. progeny of *Krapovickas et al. 19300*).

PLANTAS DE BOLIVIA

Nº. 19300

brum grandiflorum Krap.
Isotipo

Dep Tarija

Loc Ruta Tarija - Villa Montes, Yayry, 500m s.m., 40 Km W de Villa Montes

Obs

Leg A Krapovickas, L. A. Mroginski y A. Fernández 26-V-1971

HERBARIUM
OF
P. A. FRYXELL

mm in length × and 0.6 0.8 mm in width, seed coat often with slight ridges corresponding with the ribs on the mericarp surface; *chromosome number:* $2n = 24$; *pollen* 69–104 (90) μm diam, echinae 6–7 μm, apertures 24–35.

DISTRIBUTION. (Fig. 57) Known only from the type locality in the highland Chaco region of southern Bolivia, Department of Tarija, between 28 and 40 km west of Villa Montes at an elevation of 500–560 m.

PHENOLOGY AND REPRODUCTIVE BIOLOGY. Flowering April June where native, it was in flower and fruit when collected in May (local autumn). In cultivation in Texas, a seed from the type germinated five days after planting. The single plant flowered in July, 60 70 days after seed germination, then again more frequently in September–October (local late summer and autumn). The flowers opened at 10-10:30 CST and remained open until sunset (7 pm CST), a duration of 9 hours which was the longest duration of any of the species under cultivation. The stigmas remained erect and did not recurve as the flower wilted, so that in the absence of pollinators the flowers did not self-pollinate. Flowers not artificially pollinated in the greenhouse did not set fruit; those that were pollinated by hand had $<5\%$ fruit set and all seeds were inviable.

There may be incompatibility mechanisms at work. The few fruits required 30 days to mature after pollination.

The large flowers with conspicuous nectar-guides, the long duration of anthesis (for the genus), the lack of self-pollination mechanisms, and the poor seed set when artificially self-pollinated suggest a strong reliance on insect cross-pollination in its native habitat.

DISCUSSION. *Malvastrum grandiflorum* is the showiest and one of the most distinctive species of the genus. With regard to vegetative and mericarp features it can be seen to be very closely allied to *M. amblyphyllum*. Its restricted range, compared with the range of *M. amblyphyllum*, is probably a result of its dependence on insect vectors and nearly total self-incompatibility. Whether or not it once had a formerly more extensive range cannot be determined, but it does seem to be more ancient than *M. amblyphyllum* which has

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Figure 56. *Malvastrum grandiflorum* (isotype, pf).

many derived floral characters. As in *M. amblyphyllum*, *M. grandiflorum* has not reached the point of floral bract specialization, and produces fewer fruits than most of the other species in the genus.

SPECIMENS EXAMINED. **Bolivia,** TARIJA: Ysyry, 40 km. W of Villa Montes on the road to Tarija, alt. 500 m, *Krapovickas et al. 19300* (BH, G, GH, K, NY, pf, UC, US).

11. **Malvastrum amblyphyllum** R. E. Fries, Ark. Bot. **6**(2): 6, t. 2, f. 9–10. 1906. TYPE: BOLIVIA. Tarija: Fortín (Colonia) Crevaux at the Río Pilcomayo, in open woodland, April 18, 1902. *R. E. Fries 1610* (HOLOTYPE: S!, ISOTYPE: S!). *Malvastrum scabrum*

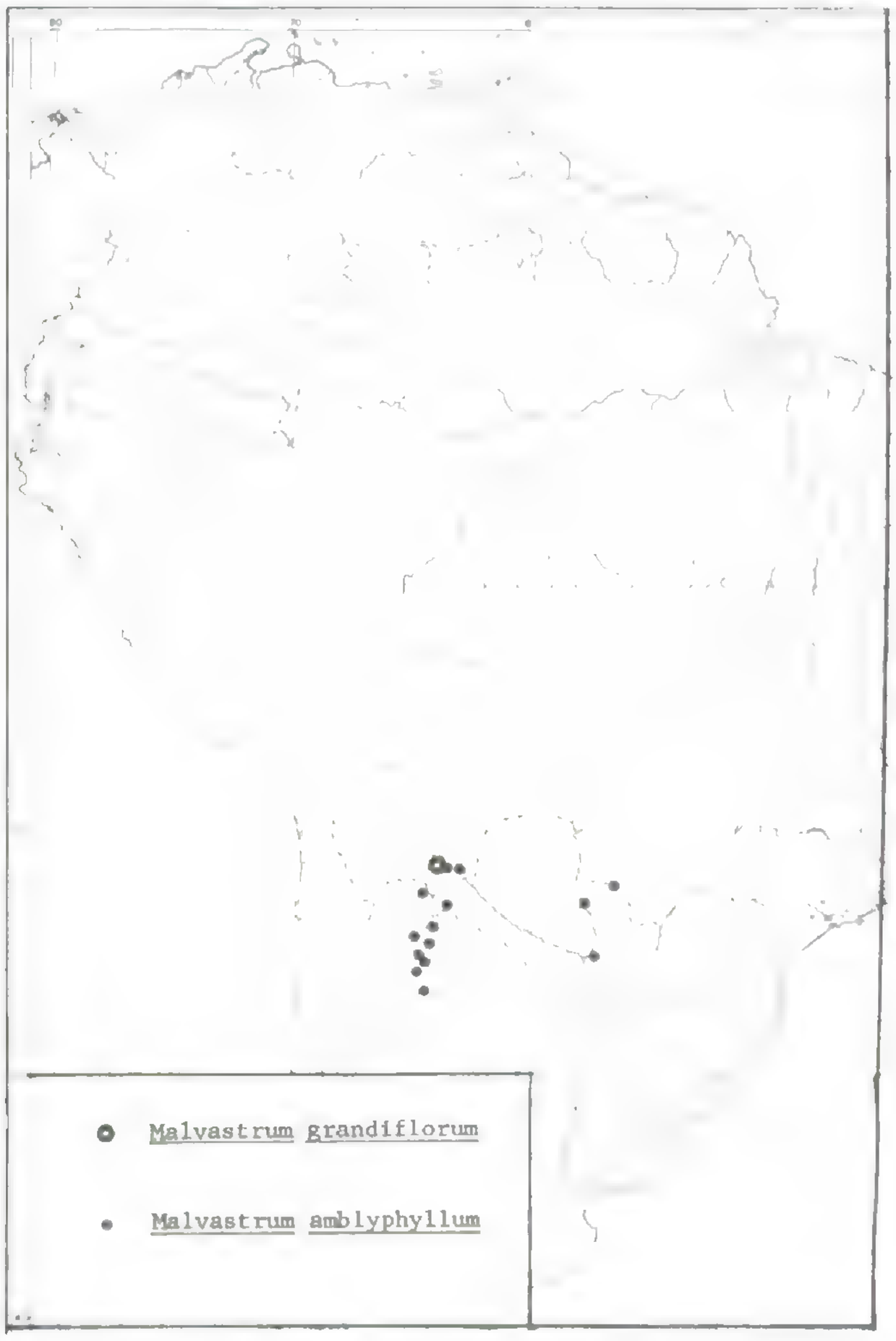


Figure 57. Distribution of *Malvastrum grandiflorum* and *M. amblyphyllum*.

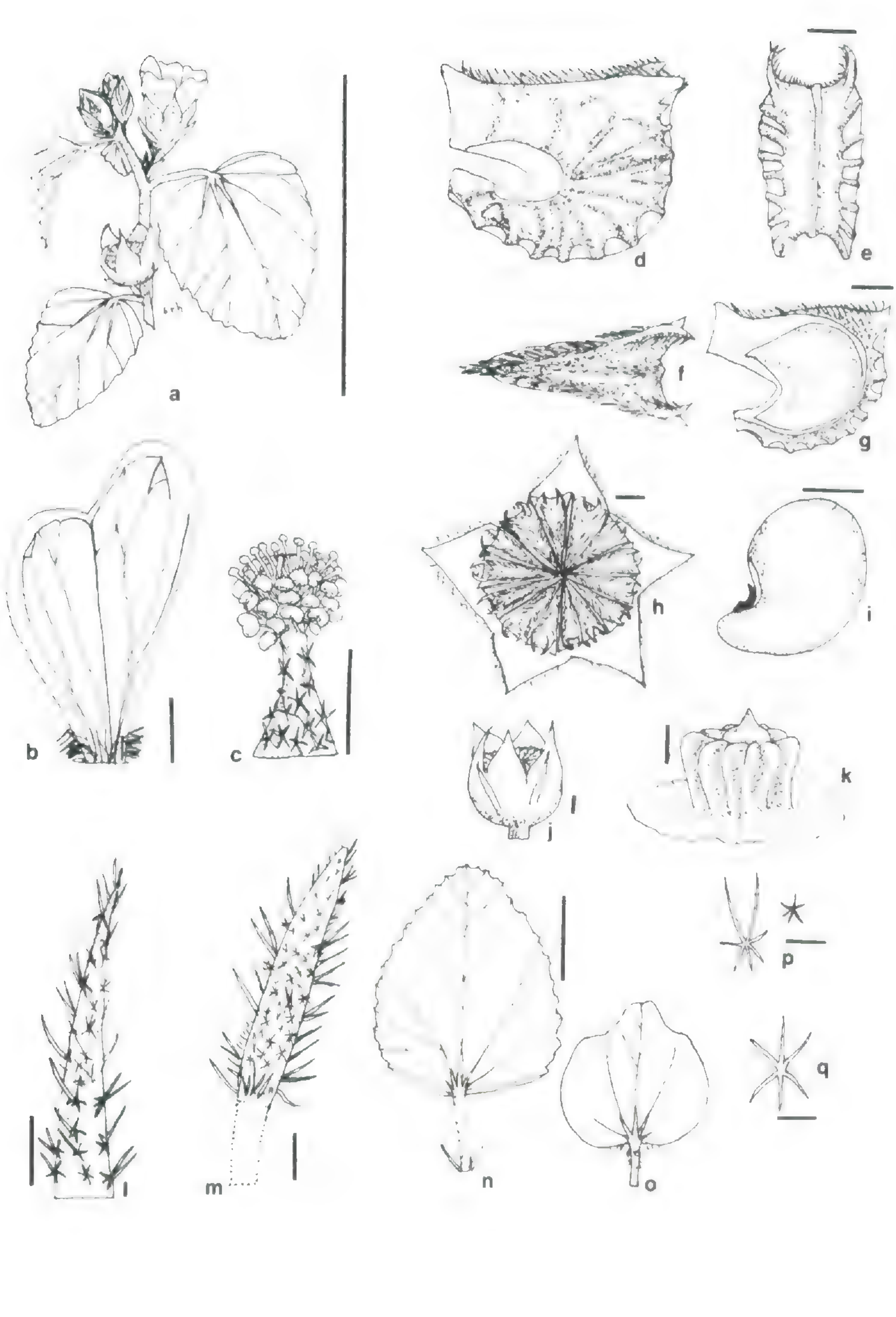
(Cavanilles) A. Gray var. *amblyphyllum* (R. E. Fries) E. Hassler, Feddes Repert. Spec. Nov. Regni Veg. **12**: 366. 1913 ("*ambliphyllum*"). Fig. 58, 59.

Malvastrum scabrum var. *paraguariense* E. Hassler, Feddes Repert. Spec. Nov. Regni Veg. **8**: 34. 1910. TYPE: PARAGUAY. "In colle calcareo pr. flumen Apa", May, 1887. *E. Hassler 21* (HOLOTYPE: G!).

Malvastrum scabrum (Cavaniles) A. Gray var. *tucumanense* E. Hassler, Feddes Repert. Spec. Nov. Regni Veg. **12**: 365. 1913. TYPE: ARGENTINA. Tucumán: District of Burrayacú. Cañada Alegre, March 12, 1909. *S. Gonzalez 19935a* (HOLOTYPE: G!; ISOTYPES: CORD, G! LIL).

Malvastrum waltheriifolium sensu Ulbrich, pro parte, Feddes Repert. Spec. Nov. Regni Veg. **13**: 510. 1915, excl. basionym. Ulbrich cites *Fries 1610*, the type of *M. amblyphyllum* as representative. *Anoda waltheriifolia* Schumann ex Ulbrich, loc. cit., excl. basionym.

Suffruticose sparsely branched perennial herb to 1.2 m tall or stunted to 0.3 m; main *stem* 5–10 mm diam at base; *branches* to 35–40 cm long, stem vesture loose to dense of (4) 5 (6)-rayed stellate hairs 1.0–1.5 mm diam; *cotyledons* 9 mm long × 9 mm wide, wide-ovate, emarginate-cuspidate at the apex, subtruncate to slightly cordate at the base, palmately 5-nerved; *stipules* (3) 4 5 (7) mm long × (0.4) 0.5 (0.8) mm wide, narrowly lanceolate to linear, acuminate; *petioles* (7) 20–35 (45) mm long; *blades* 2–2.5× longer than the petioles, (25) 30 70 (82) mm × (18) 40–60 (80) mm wide, average midstem blade 1.2–1.4× longer than wide, ovate to wide-ovate, young blades often wider than long, unlobed, base truncate broadly cuneate to slightly cordate, apex rounded to slightly acute, margin crenate-dentate with 3–4 teeth/cm, vesture of the adaxial surface loose to dense with 6-rayed stellate hairs, abaxial vesture of more dense (6) 8 10 (12)-rayed hairs; *flowers* solitary in axils of upper leaves and stipules or on short 2–4-flowered axillary branches or terminal spicate racemes with shortened internodes; *pedicels* (0.5) 1–2 (5) mm long increasing typically from 1 mm at anthesis to 4 mm in fruit; *involucel* of 3 narrowly lanceolate to linear bracteoles (5) 6–7 (8) mm long × (0.5) 1.0 mm wide, united to calyx 1.5 mm below; *calyx* united 1/4 to 1/3 its length, 7 8 mm from pedicel to lobe apex to 9–11 mm in fruit, somewhat narrowly campanulate at anthesis, lobes erect, deltate, acuminate-cuspidate, (5) 7 8 (9) mm long × 3–4 mm wide, tomentose on the abaxial surface with small or large 5 8-rayed stellate hairs 0.3 mm or 1.5 mm diam, ca. 1/3 of the hairs with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2–4 enlarged and thickened rays apically directed, adaxial surface of lobes pubescent with downy minute simple hairs medially and with minute stellate hairs towards the margins; *corolla* yellow, petals asymmetrically bilobed, (6) 8–10 (12) mm long × (3.5) 4–5 mm wide slightly exceeding calyx by 2 mm, campanulate at anthesis and not spreading, claws pubescent at base with coarse stellate hairs; *androecium* with (26) 35–36 (70) stamens, filament tube 2–2.5 mm long, pubescent with coarse 5–6-rayed stellate hairs, free portion of filaments (0.5) 1 mm long, anthers 0.5 mm long after dehiscence; *gynoecium* with (11) 14–15 (16) loosely coherent carpels, style branching 2 mm above the columella, each branch terminated by a globose expanded stigma raised above the anthers by 0.5 mm not recurved at flower wilt, ovary surface densely pubescent with centrally directed simple appressed hairs; *schizocarps* 9–11 mm diam including ornamentation; *mericarps* (11) 13–15 (16), 3.0–4.5 mm in height × (3) 4–5 mm in length × 2 mm in width including ornamentation with a proximal-apical cusp 0.1–1 mm long and 2 distal-apical cusps 0.5–1 mm long, the latter distinctly separate but curved towards one another, lateral faces with conspicuously opaque ribs extending into a thin translucent winged border extending 0.5 mm from the mericarp body, distal surface with a conspicuous raised medial line, vesture restricted to the apical surface of coarse strigose rigid proximally directed appressed simple hairs 0.8 mm long, proximal-apical region thin solid woody, completely indehiscent, endoglossum absent, readily separating from the receptacle at maturity; *seeds* slightly narrowed in the basal half below the hilum, 2.5 mm in height × 2 mm in length × 0.7 mm in width, seed coat dark brown; *chromosome number:* $2n = 24$; *pollen* 62–79 (70) μm diam, echinae 4–5.1 μm, apertures 15–30.

Figure 58. *Malvastrum amblyphyllum*. a. Habit, scale = 5 cm. b. Petal, scale = 2 mm. c. Stamens, styles, and stigmas, scale = 2 mm. d.–f. Mericarp, lateral, distal, and apical views, scale = 1 mm. g. Mericarp, internal view, scale = 1 mm. h. Fruit, apical view, scale = 2 mm. i. Seed, scale = 1 mm. j. Calyx in fruit, vesture not indicated, scale = 2 mm. k. Columella and carpocrater, scale = 0.5 mm. l. Stipule, scale = 1 mm. m. Bracteole, scale = 1 mm. n. Leaf, scale = 2 cm. o. Cotyledon, scale = 5 mm. p. Calyx vesture, scale = 0.5 mm. q. Leaf vesture, adaxial surface, scale = 0.5 mm. (All drawn from progeny fo *Krapovickas et al. 18558*).

Herb. Brasil. Regnell. Musei bot. Stockholm.
Exped. Swec. in reg. Chaco Andic
Rob. E. Fries.

DISTRIBUTION. (Fig. 57) Restricted to the Chaco region of southeastern Bolivia, central and northern Paraguay, and northwestern Argentina, at elevations of 100–1000 m.

PHENOLOGY AND REPRODUCTIVE BIOLOGY. Flowering February June (summer–autumn where native). In cultivation in Texas seeds of *Krapovickas et al. 18558* germinated after four days and first flowered in October and November (local autumn) after 120 days of growth. The flowers were produced for less than 30 days, each lasting a single day and open for two hours (10:30–12:30 CST, opening one hour earlier on warmer days, the variables apparently being light intensity and temperature). Under cultivation the flowers always self-pollinated, the pollen usually being released directly onto the stigmas. Self-pollination is also likely the predominant means of reproduction in wild populations even with insect visitors due to the close proximity of the anthers and stigmas and the brief flowering time. Fruits ripened in 29 33 days after anthesis. The seeds are viable for at least 7 years.

DISCUSSION. Fries was the first to note the unusual features of this species. Hassler chose to describe the plant as *Malvastrum scabrum* var. *tucumanense*, and a non-fruiting specimen was called var. *paraguariense*. *Malvastrum amblyphyllum* is distantly allied (along with *M. grandiflorum*) to *M. tomentosum*. *Malvastrum amblyphyllum* probably had a progenitor similar to *M. grandiflorum* but developed along a reductional pathway, becoming an autogamous species. Its greater range demonstrates its degree of success with this mechanism. Despite autogamy, the species is diverse with respect to stamen number and inflorescence density but the latter character seems to be correlated with plant maturity.

SPECIMENS EXAMINED. **Paraguay.** CONCEPCIÓN: fields, hillsides, San Salvador, *Rojas 2602* (G, pf); Saavedra, Chaco Paraguayo sandy soil, *Rojas 7041* (G); ASUNCIÓN: low hills, Luque, *Rojas 1685* (G, pf); río Apa, *Hassler 21* (G); Pycuiba, *Rojas 7278* (BH, G); San Salvador, *Balansa 1624* (BH, G). **Bolivia.** SANTA CRUZ: Río Parapetí, *Krapovickas 9482* (TEX); Cordillera, 22 km N of Gutiérrez, *Krapovickas & Schinini 31452* (G); 4 km S of Roboré, *Krapovickas & Schinini 36499* (MICH, srh); Santiago, *Krapovickas & Schinini 36470* (srh); TARIJA: Bajada de San Simón, 15 km E of Entre Ríos, Tarija-Villa Montes road, *Krapovickas 19127* (pf); CHUQUISACA:

Figure 59. *Malvastrum amblyphyllum* (holotype).

prov. Azero, 5 km N of Carandayti, *Krapovickas & Schinini 31229* (MICH); Tapirendita, 15 km E of Villa Montes, *Krapovickas et al. 19336* (TEX, UC). **Argentina.** JUJUY: San Pedro de Jujuy, railroad right-of-way, *Krapovickas 4765* (DAO); SALTA: Dpto. Metán, río Juramento, ruta no. 34, *Krapovickas et al. 18558* (pf, TEX, UC, WIS); Dpto. Metán, Esteco, roadside, *Krapovickas et al. 27984* (G, MO, UC): Dpto. Orán, Padre Lozano railway station, *Krapovickas 1322* (NY); Dpto. Gral. S. Martin, Campo Durán, *Krapovickas et al. 19494* (pf); 0 3 km west of Cabeza del Buey, road to Salta, *Krapovickas 7246* (WIS); TUCUMÁN: Burruyacú, Cañada Alegre, *Gonzalez 19935a* (G).

To be concluded in Vol. 84, No. 839 (July, 1982).

THE TAXONOMIC STATUS OF *OXYPOLIS GREENMANII* (APIACEAE)

WALTER S. JUDD

Oxypolis greenmanii was first described by Mathias and Constance (1942), although it had been collected much earlier (see *Chapman*, Aug. 1896, MO and *Small & West,* Aug. 1935, FLAS), and the specific epithet refers to Mr. J. M. Greenman who first recognized the distinctness of this taxon. It has been only little collected but is actually rather abundant in the wetlands within a very limited region of the Florida panhandle (Figure 1). Mathias and Constance (1942) noted that *O. filiformis* (Walter) Britton, a widespread coastal plain species extending from Florida northward to North Carolina and westward to Louisiana, was likely the closest relative of *O. greenmanii* Math. & Const. Both species have their leaves reduced to articulated (i.e., septated) phyllodes. Only the rare *O. canbyi* (Coult. & Rose) Fernald also possesses phyllodial leaves. However, this species has shorter phyllodial sheathes and fruits with thickened corky wings (see Mathias and Constance, 1949; Rodgers, 1950). Mathias and Constance (1942) reported that "In general, *O. Greenmanii* may be distinguished from *O. filiformis* by its greater stature, much larger phyllodes, more numerous rays and deep purple flowers." Godfrey and Kral (1958) also reported that "*Oxypolis greenmanii* is notably distinct from *O. filiformis* ...". However, recent field investigations by the author and Kent D. Perkins have indicated extensive intergradation between these two taxa, and many intermediate populations are now known. Thus the taxonomic status of *O. greenmanii* is here reconsidered in connection with a study of the morphological, ecological, and geographical variability within this taxon and *O. filiformis*.

The range of morphological variation exhibited by *Oxypolis filiformis* and *O. greenmanii* was investigated throughout the geographical range of the two taxa, with special emphasis being given to (1) plant height, (2) basal phyllode size and shape, (3) prominence of phyllodial articulations, (4) number of primary rays per umbel, and (5) flower color, since these characters either had been used by earlier botanists in distinguishing these taxa or had been discovered to be particularly variable during preliminary field studies of the group. The pattern of variation in these (and other)

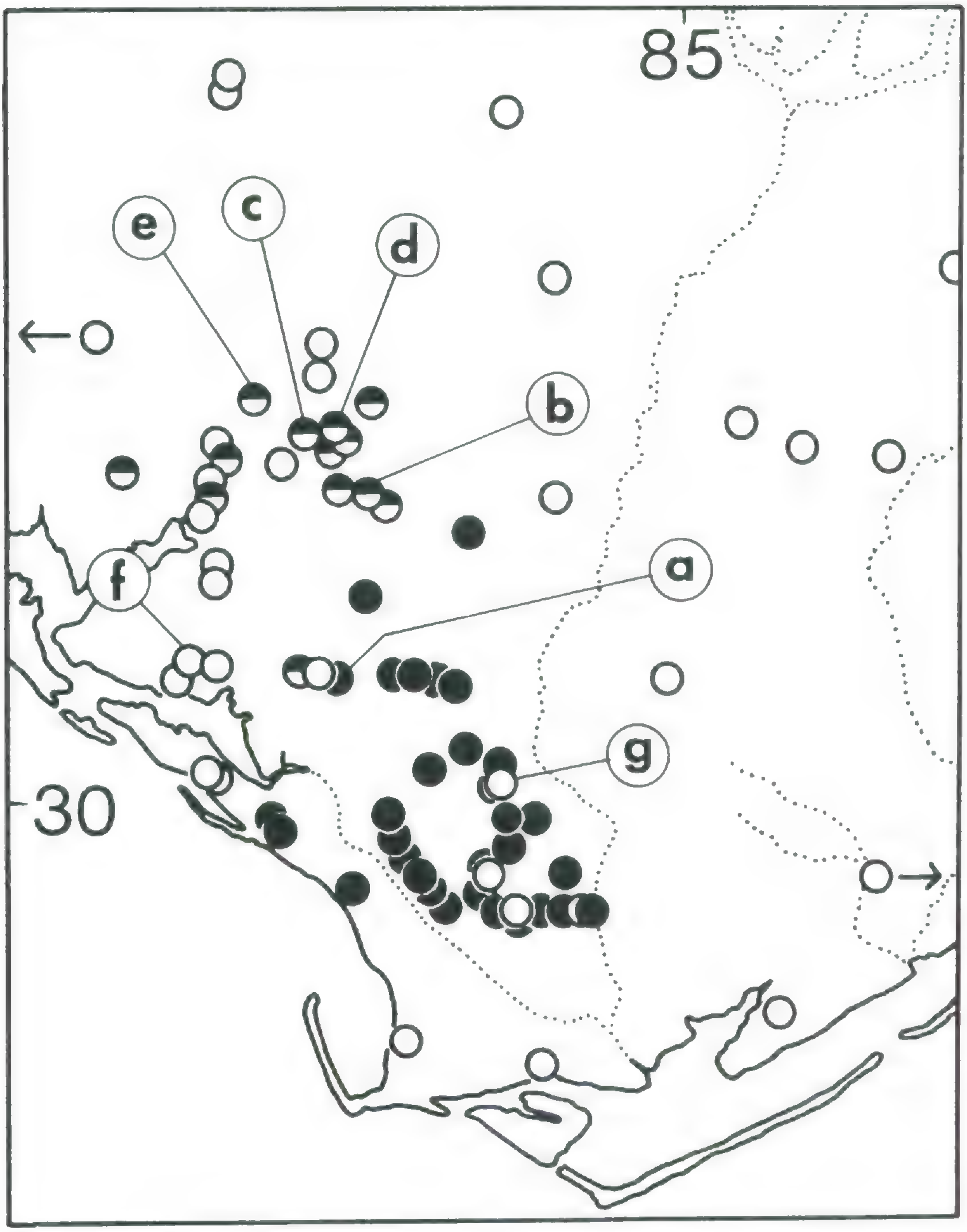

Figure 1. **Distribution of phyllodal-leaved Oxypolis in Gulf, Bay, and Calhoun counties, and in adjacent areas of Florida panhandle.** Open circle = population of *Oxypolis filiformis;* dot = population of *Oxypolis greenmanii;* half-shaded circle = intermediate population. For a presentation of morphological variability of labeled populations (a g) see Figures 3–7 and discussion in text.

characters was determined through a study of herbarium specimens from throughout the range of the taxa, and by detailed field studies of seven populations of *Oxypolis* from Bay and Gulf counties, Florida.

Throughout most of its range *Oxypolis filiformis* was found to be characterized by individuals with at least slightly keeled and more or less obscurely articulated basal phyllodes and white flowers. In contrast, most individuals of *O. greenmanii* may be distinguished by their often larger and conspicuously articulated basal phyllodes that are round to elliptic in cross-section, i.e., not keeled, and deep to pale purple flowers (Figure 2). Great variation in height and

Table 1. **Variation in selected morphological characters in Oxypolis greenmanii and O. filiformis**

character	O. greenmanii	O. filiformis
Plant height	0.4–2.5 (−3) m	0.3–1.5(−2.5) m
Basal phyllode width[1]	ca. 4.5–17 mm	ca. 2–8 mm
Basal phyllode breadth[1]	ca. 4–17 mm	ca. 1–6 mm
Basal phyllode shape[1] (in cross-section)	round or elliptic, not keeled	flat and strongly keeled to elliptic and only slightly keeled
Phyllode articulations	± conspicuous	± inconspicuous
Flower color	deep to pale purple	white (to very slightly pink tinged)
Number of primary rays per umbel[2]	ca. 7 30	ca. 5–25

[1] Measured at apex of phyllode sheath; width = distance from adaxial to abaxial side of phyllode when cut in cross-section; breadth = distance across basal phyllode when cut in cross-section, i.e., perpendicular to width.
[2] Measured on largest umbel per plant (usually the terminal umbel).

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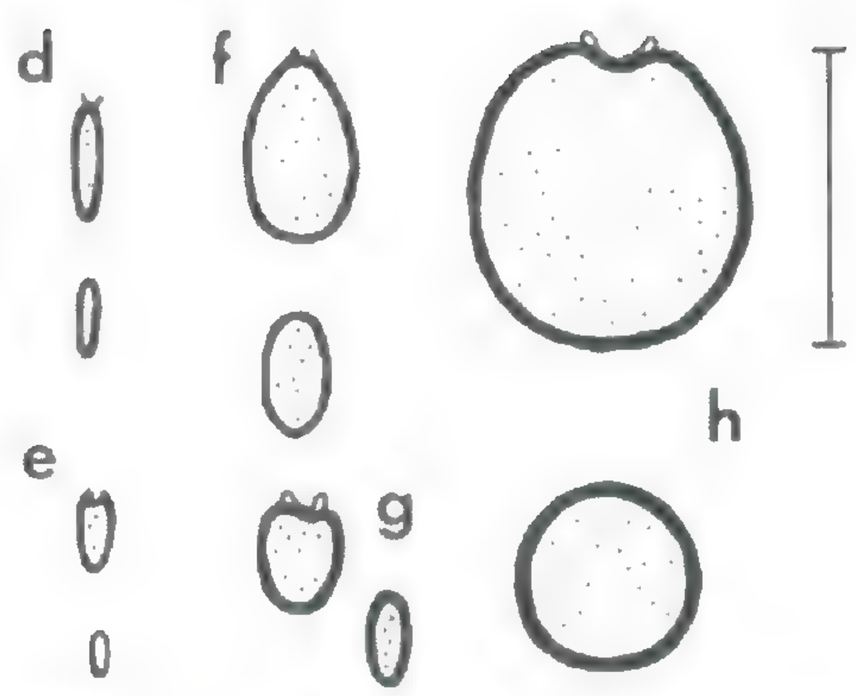
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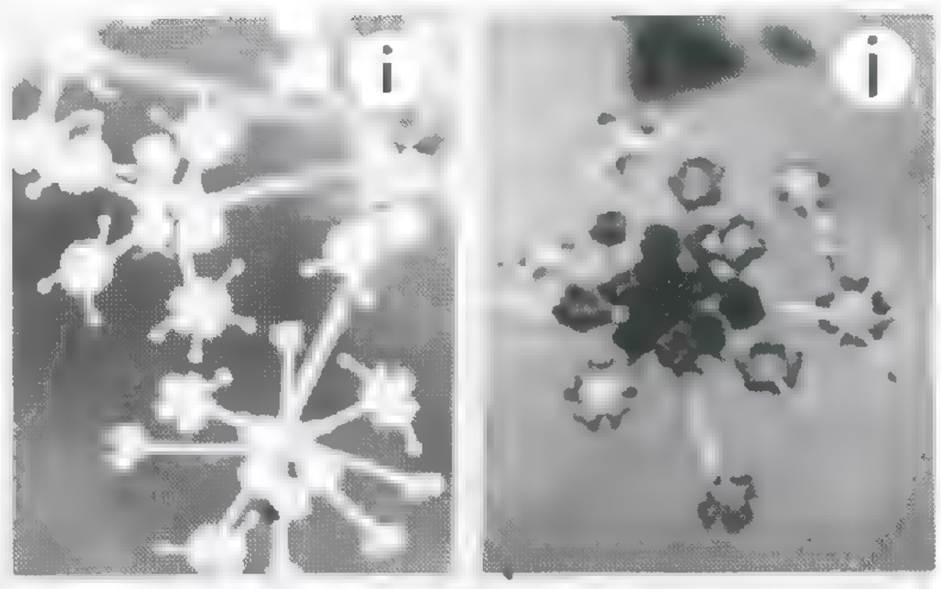
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"robustness" of plants exists in both taxa (Table 1). Similarly, the number of primary rays per umbel is extremely variable, and is thus of only very limited use in distinguishing the taxa (Table 1). (The use of both features by Mathias and Constance (1942, 1945) likely resulted from their very incomplete knowledge of the range of variability within this group.) It should also be noted here that flower color is not closely correlated with vegetative pigmentation; thus plants with deeply purple stems and phyllodes may have white flowers and vice versa. Populations referrable to *O. greenmanii* were found to be restricted to Gulf, Calhoun, and Bay counties, Florida. Such populations are most characteristic of *Hypericum* bogs (e.g., *Hypericum chapmanii, H. brachyphyllum, H. nitidum, H. fasciculatum*) but also occur in wet *Pinus elliottii* flatwoods, open *Taxodium ascendens* swamps, wet marshy areas, and disturbed roadside ditches. In contrast, *O. filiformis* is abundant throughout Florida. In the Florida panhandle this taxon was found to occur most frequently in sedge-grass-pitcher plant bogs or marshes and moist roadside ditches, but it can occur in wet *Pinus elliottii* flatwoods as well as *Taxodium ascendens* swamps. Within the region occupied by *O. greenmanii, O. filiformis* is rather uncommon and is mainly restricted to disturbed habitats along roadsides. However, many morphologically intermediate and taxonomically puzzling populations of *Oxypolis* were discovered in the northeastern portion of Bay County and in adjacent areas of Gulf County (Figure 1). These populations occur in both grass-sedge marshes and *Hypericum* bogs. This region marks the extreme northwestern extent of the range of *O. greenmanii,* and is characterized by many morphologically interesting *Oxypolis* populations, each of which is distinghished by a more or less distinctive character combination (i.e., genetic composition). Populations occur which are composed exclusively of plants that have robust, unkeeled basal phyllodes and white flowers. Other populations are composed of uniformly unkeeled plants which vary in flower color from white to pink or

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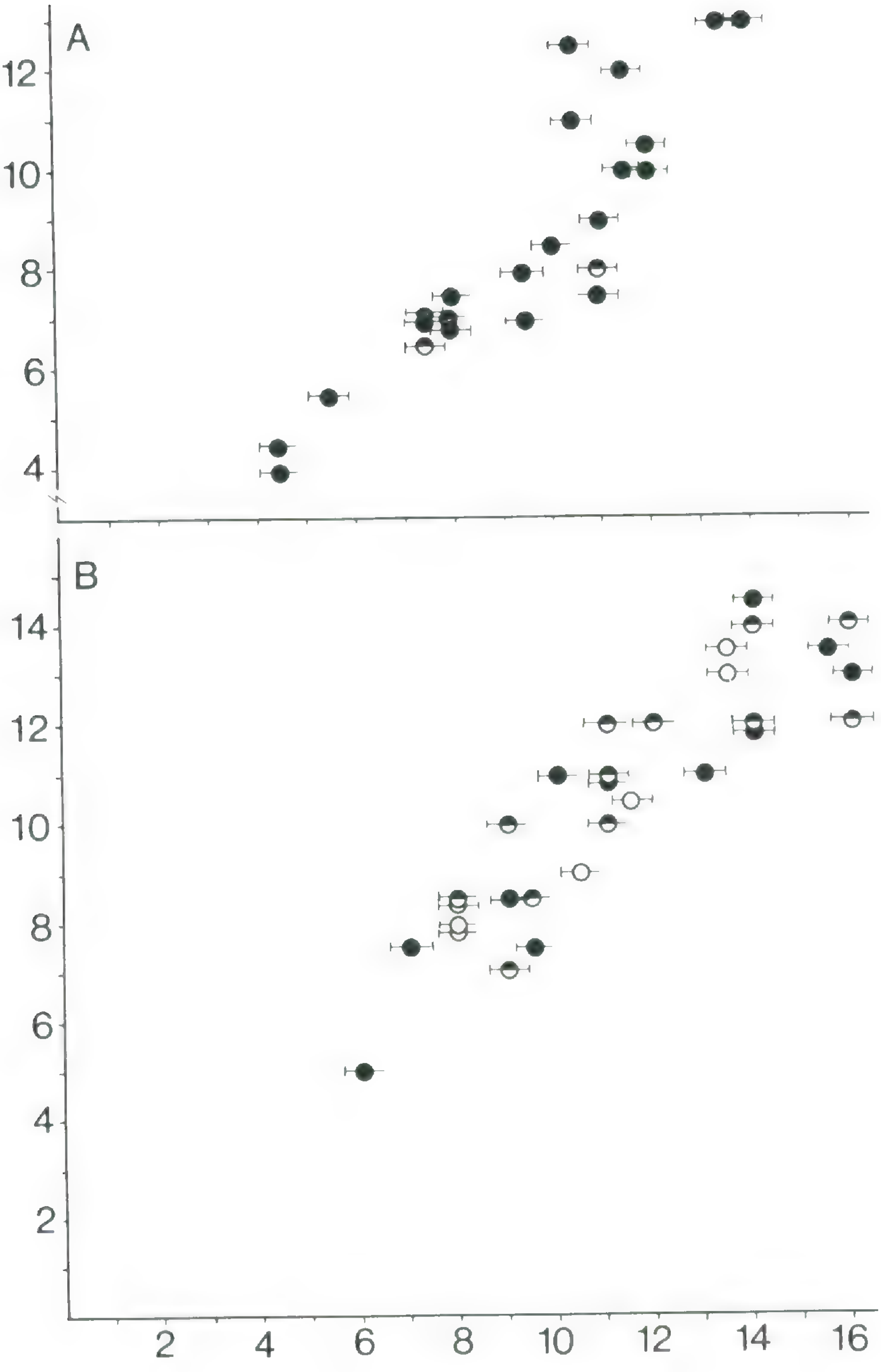
Figure 2. **Distinctive morphological characters of Oxypolis filiformis and O. greenmanii. a,** basal phyllodes of *O. greenmanii;* **b,c,** basal phyllodes of *O. filiformis.* **d–h,** cross-sections of basal phyllodes at apex of sheath, and midway between sheath and phyllode apex, scale = 15 mm: **d,e,** *O. filiformis;* **f,g,** intermediate plants; **h,** *O. greenmanii.* **i,j,** flowers: **i,** *O. filiformis* (white); **j,** *O. greenmanii* (purple).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purple, while still others are uniform in flower color but vary in the size and shape (in cross-section) of the basal phyllodes (see Figures 3 5). These populations completely bridge the morphological gap between *O. filiformis* and *O. greenmanii* as traditionally delimited. Four of these intermediate populations (indicated in Figure 1) were studied in detail in the field by recording information on flower color, and on size (both width and breadth), prominence of keel development, and conspicuousness of articulations of the basal phyllodes on ca. 15–30 individuals per population. Data were recorded in the field since all vegetative characters listed above are either destroyed or seriously distorted in pressed and dried specimens. In addition, specimen drying somewhat obscures flower color. However, voucher specimens were made from each population. Two additional populations were similarly studied one of *O. greenmanii* from a region removed from populations of *O. filiformis*, and one of *O. filiformis* geographically distant from any population of *O. greenmanii*. These populations served as "standards" or indicators of the morphological variability in typical populations of both taxa.

The results of these field investigations are presented in Figures 3 5. These scatter diagrams clearly demonstrate the distinctive morphological composition of each population. They also indicate that some populations tend toward *O. filiformis* and others toward *O. greenmanii*. It is easily seen that the degree to which a population

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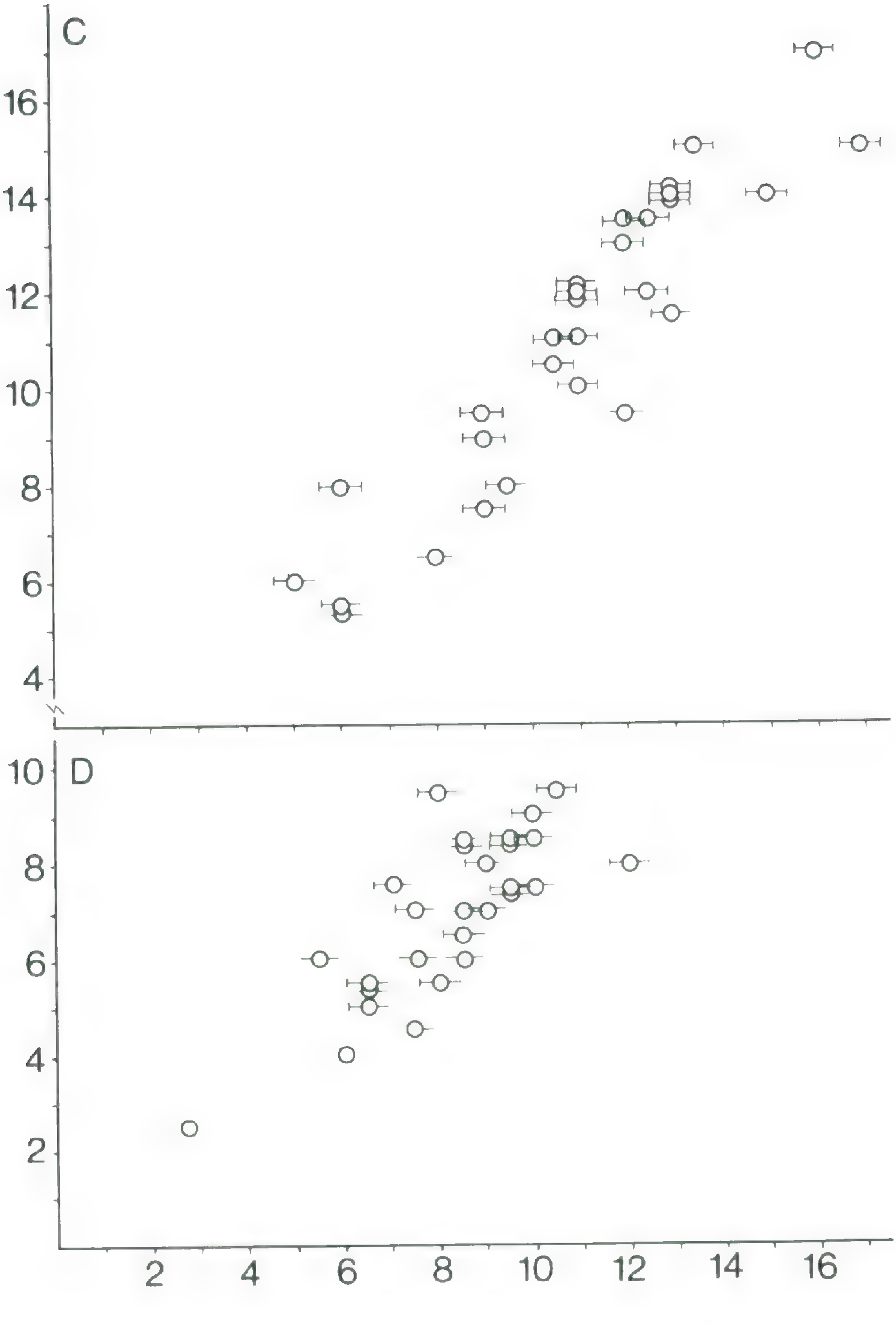
Figure 3. **Variation in certain morphological characters within selected Oxypolis populations of Gulf, Bay, and Calhoun counties, Florida.** Open circle = white flowered plant; half-shaded circle = ± pink flowered plant; dot = purple flowered plant. Full tail to left = basal phyllodes not keeled; half tail to left = phyllodes slightly keeled; no tail to left = phyllodes keeled. Full tail to right = phyllode articulations conspicuous and impressed; half tail to right = articulations inconspicuous; no tail to right = articulations slightly visible and raised. Horizontal axis = width of basal phyllodes in mm (i.e., distance from adaxial to abaxial side of phyllode when cut in cross-section at apex of sheath). Vertical axis = breadth of basal phyllodes in mm (i.e., distance across basal phyllode when cut in cross-section; perpendicular to width).

A. *Oxypolis greenmanii* population; Gulf Co., along Rt. 22, ca. 0.9 mi. E of Gulf/Bay County line, S18, T4S, R11W, in *Hypericum chapmanii* bog (with *H. brachyphyllum*) *Judd & Perkins 2321* (FLAS). **B.** Intermediate population; Calhoun Co., along Scotts Ferry Rd. ca. 4.5 mi. E of jct. with Rt. 231, S5, T2S, R11W, in *Hypericum fasciculatum* bog, *Judd & Perkins 2729* (FLAS).

For further information see Figure 1 and discussion in text.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resembles "standard" *O. greenmanii* is roughly correlated with its geographical distance from the Gulf-Calhoun-Bay county area in which this taxon occurs. Thus population "E" is morphologically closest to "standard" *O. filiformis* while population "B" is closest to *O. greenmanii* (see Figures 1, 3, and 5). If the "key" characters of the basal phyllodes and flowers are applied to the individuals composing these populations, some, i.e., "E" and "D", are seen to be composed of plants falling within the variation range of *O. filiformis* along with intermediate individuals, i.e., plants with white flowers and unkeeled or only very slightly keeled basal phyllodes, while population "B" is composed of plants falling within the range of variation of *O. greenmanii* along with intermediate individuals, in this case, white to pink flowered plants with more or less unkeeled basal phyllodes. Population "C" is composed of exclusively intermediate plants which possess the white flowers characteristic of *O. filiformis* and the large, unkeeled basal phyllodes characteristic of *O. greenmanii*! (See Figure 4). The morphological gap between *O. greenmanii* and *O. filiformis* is completely bridged using only these populations. However, many other similar intermediate populations exist within this area, resulting in a total morphological continuum between the two taxa (Figure 6).

It is important to note that the sets of characters usually distinguishing these two taxa are not correlated within these populations. Thus plants with robust, unkeeled basal phyllodes and white flowers are common, and within a population the plants with smaller phyllodes are not necessarily more frequently white flowered. Plants with slightly keeled leaves and purple flowers also occur. Although these intermediate populations show variation in characteristics that are usually invariant within most populations of either *O. filiformis* or *O. greenmanii,* they are not extremely

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Figure 4. **Variation in certain morphological characters within selected Oxypolis populations in Gulf, Bay, and Calhoun counties, Florida.** For explanation of symbols and graph axes see Figure 3.
C. Intermediate population; Bay Co., along Rt. 231, 1.8 mi. N of jct. with Rt. 388 (N of Youngstown), S15, T1S, R12W, in *Hypericum fasciculatum* swamp, *Judd & Perkins 2400-2405, 2714* (selected specimens at FLAS).
D. Intermediate population; Bay Co., along Linger-Longer Rd. ca. 1.4 mi. E of jct. with Rt. 231, S14, T1S, R12W, in grass-sedge marsh at edge of pinelands with *Sarracenia* and *Cyrilla, Judd & Perkins 2718* (FLAS).
For further information see Figure 1 and discussion in text.

variable, that is, such populations are *not* composed of individuals referrable to typical *O. greenmanii* and *O. filiformis* along with a host of intermediate plants. Rather, as described above, the populations exhibit a range of morphological variation comparable with that of "standard" populations of both taxa (compare Figures 3–5). These populations are, in fact, often uniformly intermediate in

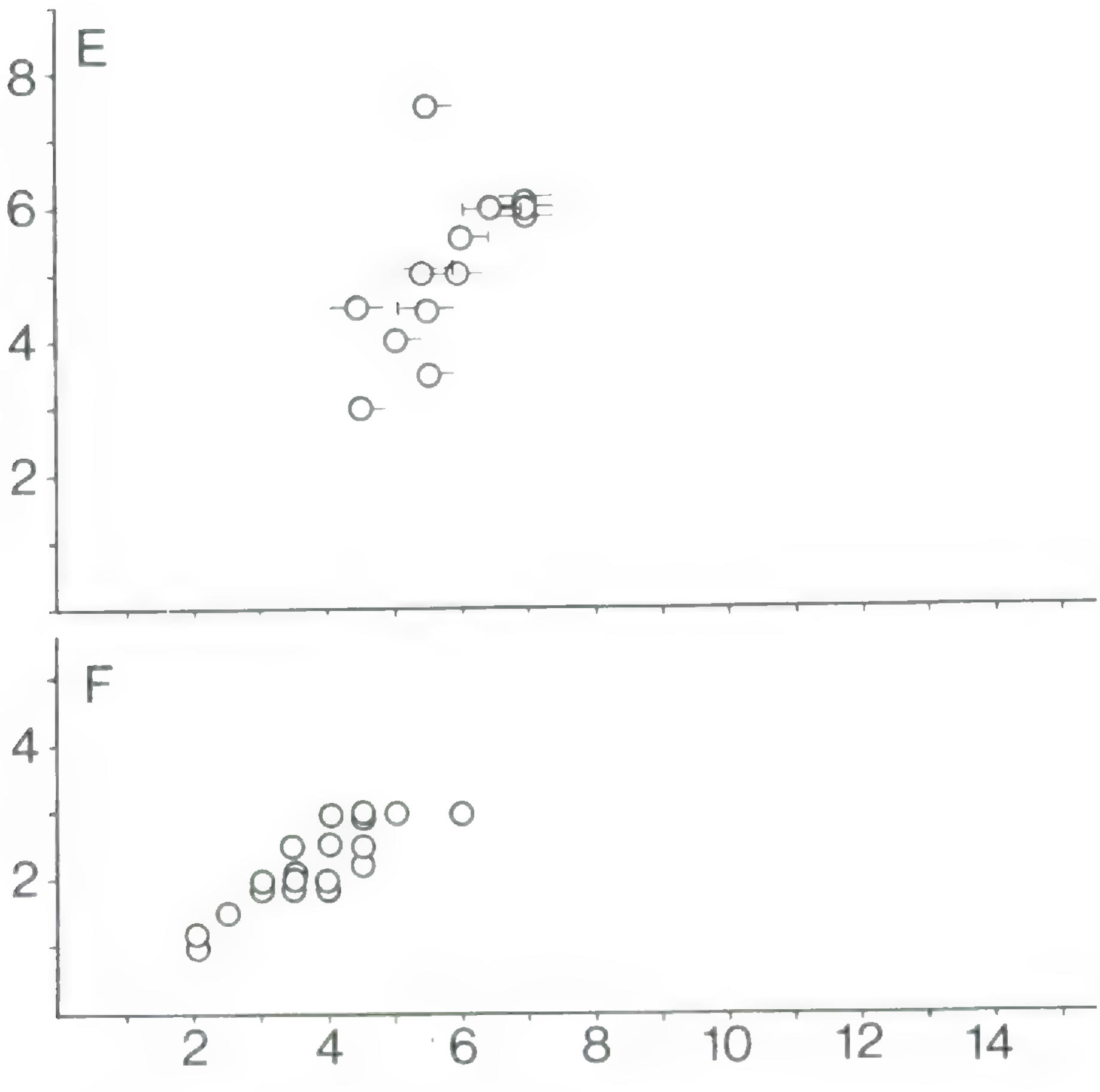

Figure 5. **Variation in certain morphological characters within selected Oxypolis populations in Gulf, Bay, and Calhoun counties, Florida.** For explanation of symbols and graph axes see Figure 3.
E. Intermediate population; Bay/Washington County line, along Rt. 20, 2.8 mi. E of Econfina Creek, S1, T1S, R13W, in *Hypericum fasciculatum* bog, *Judd & Perkins 2738* (FLAS).
F. *Oxypolis filiformis* population; Bay Co., jct. of Callaway Bayou and Rt. 22, S9, T4S, R13W, *Judd & Perkins 2428-2432* (selected specimens at FLAS).
For further information see Figure 1 and discussion in text.

several characters (see scatter diagram of population "C" in Figure 4) and may therefore be placed at definite locations along a continuum of variation connecting typical *O. greenmanii* with typical *O. filiformis*. All individuals in the studied populations were flowering and fruiting vigorously and all plants tested were found to be highly fertile (ca. 90% to nearly all pollen grains stained with cotton-blue in lacto-phenol). Such evidence would seem to discount the possibility of a hybrid origin for these populations.

However, many extremely variable *Oxypolis* populations do exist within the geographic range of *O. greenmanii* (see Figures 1 and 7). These populations, unlike those discussed above, are limited to disturbed wet roadside habitats, and are extremely variable, being composed of typical *O. filiformis* and *O. greenmanii* along with a nearly complete selection of intermediate plants. Within these populations there is a clear correlation between degree of keeling, size of basal phyllodes, and flower color (Figure 7). The variation pattern of such populations is probably best explained as a result of the crossing of plants occupying the extremes of the morphological continuum described above. Most of the presumed hybrid plants composing these variable populations are highly fertile (ca. 90% to nearly all pollen grains stained with cotton-blue in lacto-phenol), however, one had only ca. 50% stained grains. All plants falling within the variation range of either *O. greenmanii* or *O. filiformis* are very fertile (ca. 95% to nearly all grains stained). Both *O. greenmanii* and *O. filiformis* have a chromosome number of $n = 14$ (Bell & Constance, 1957, 1960), flower together, and seem not to be isolated by cytological or seasonal factors. Pollinator differences may lead to partial isolation since the white flowers of *O. filiformis* are visited by many unspecialized insects, while the purple flowers of *O. greenmanii* are visited mainly by various wasps (see Lindsey & Bell, 1981). However, we noted both tuphiid and vespid wasps (*Myzinum* and *Polistes*) visiting the flowers of both taxa and the effectiveness of this isolating mechanism is called into question by the many "hybrid" populations in existence.

It is evident from the data presented above that *Oxypolis greenmanii* can no longer be maintained as a distinct species, but should instead be considered a subspecies of the widespread *O. filiformis*. This taxonomic change is necessitated because the two taxa are evidently completely interfertile (breeding studies would be valuable here) and are connected by an extensive series of

intermediate populations. The most useful characters in distinguishing the subspecies are flower color (purple in ssp. *greenmanii vs.* white in ssp. *filiformis*) and basal phyllode morphology (± large, unkeeled, and conspicuously articulated in ssp. *greenmanii vs.* smaller, » keeled, and inconspicuously articulated in ssp. *filiformis*). Living (or liquid-preserved) material is required for positive identification (especially of fruiting material) since all known taxonomically useful characters of the basal phyllodes are either destroyed or seriously distorted during pressing and drying.

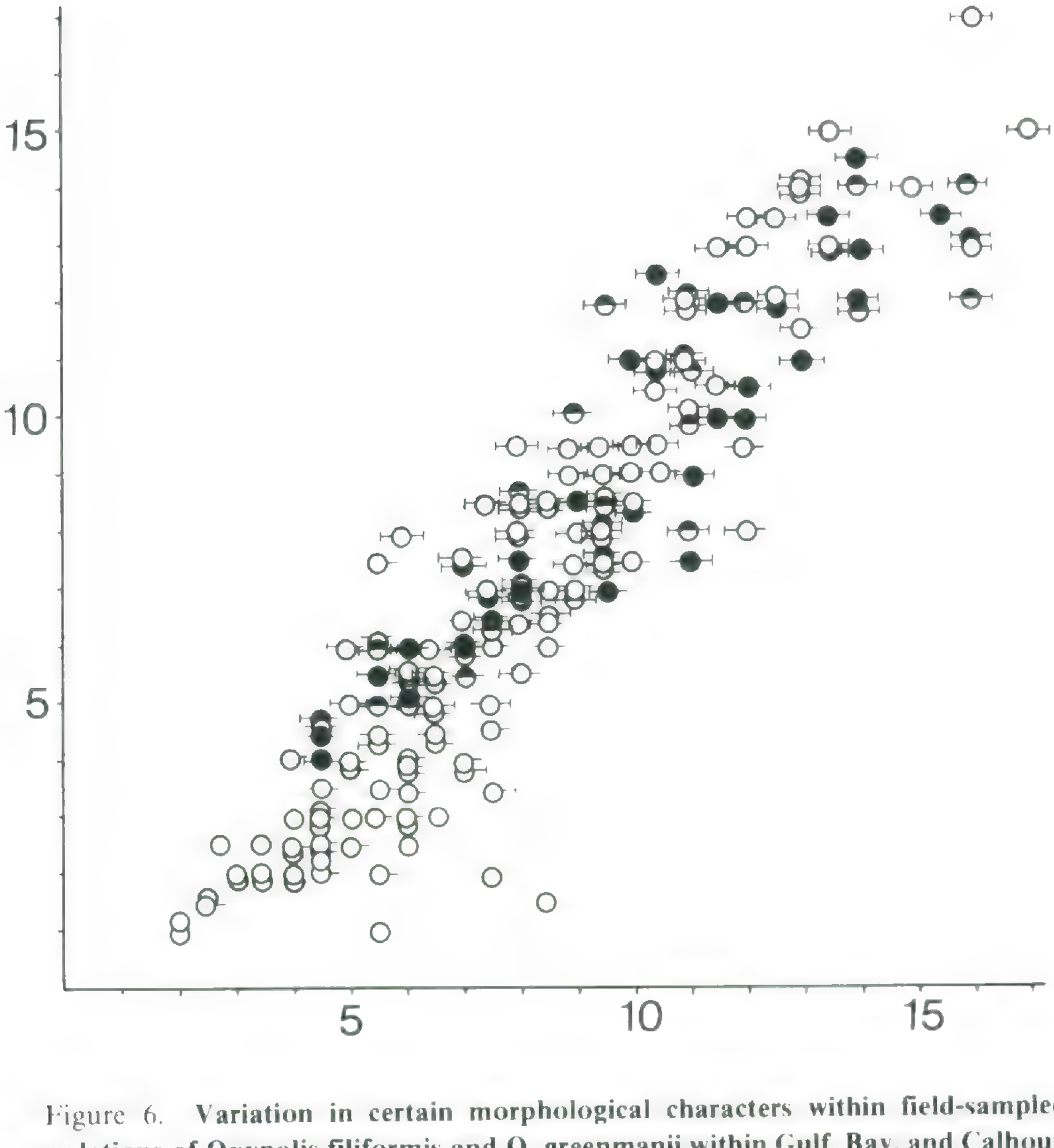

Figure 6. **Variation in certain morphological characters within field-sampled populations of Oxypolis filiformis and O. greenmanii within Gulf, Bay, and Calhoun counties, and adjacent regions of the Florida panhandle.** (Obviously "hybrid" populations have been excluded.) See Figure 3 for explanation of symbols and graph axes.

Oxypolis filiformis (Walter) Britton ssp. **greenmanii** (Math. & Const.) Judd, *comb. et stat. nov.* (*Oxypolis greenmanii* Math. & Const. Bull. Torrey Bot. Club **62**: 152. 1942.)

REPRESENTATIVE SPECIMENS: UNITED STATES, **Florida.** BAY CO.: ca. 1 mi. E of Rd. to Baker Point & 1 mi. N of U. S. 98, Tyndall Air Force Base, S5, T6S, R12W, *Judd & Perkins 2440* (FLAS); Fla. 22, 5.2 mi. E of jct. with Rt. 167, S14, T4S, R12W, *Judd and Perkins 2741* (FLAS). CALHOUN CO.: 1.4 mi. N of jct. of Fla. 73 & Rt. C-392, ca. 3 mi. N of Kinard, S15, T2S, R10W, *Judd & Perkins 2390* (FLAS); Scotts Ferry Rd., ca. 4.5 mi. E of jct. with U. S. 231, S5, T2S, R11W, *Judd & Perkins 2729d* (FLAS); 12 mi. W of Wewahitchka (Tenmile Swamp Quad), T3S, R11W, *McDaniel 5721* (FSU). GULF CO.: Fla. 71, 13–14 mi. N of Port St. Joe, *Godfrey & Jervis 53690* (FSU); White City Rd., 2.6 mi. S of jct. with Fla. 381, S14, T6S, R9W, *Judd & Perkins 2328* (FLAS); just W of Howard Creek Subdivision, S1, T7S, R9W, *Judd & Perkins 2348* (FLAS); ca. 1 mi. N of jct. of Rt. 381-A & Fla. 71, ca. 6 mi. S of Wewahitchka, S30, T5S, R9W, *Judd & Perkins 2368* (FLAS); Rd. 20, 4 mi. SE of Overstreet, S14, T6S, R11W, *Judd & Perkins 2379* (FLAS); 4.5 mi. NE of Early, *Thorne 17317* (FLAS, FSU).

Oxypolis filiformis subspecies *filiformis* and *greenmanii* are probably isolated by a combination of ethological (pollinator differences), ecological, and geographical factors, with ssp. *filiformis* being essentially replaced in the wetland habitats of Gulf county by ssp. *greenmanii*, with ssp. *greenmanii* occurring mainly in *Hypericum* bog habitats *vs.* grass-sedge marsh habitats for ssp. *filiformis*, and with the two subspecies differing in flower color (and thus attracting a somewhat different pollinator spectrum—see Lindsey and Bell, 1981). It is of interest that the morphologically intermediate populations are adjacent to and partially overlap the northwestern portion of the range of ssp. *greenmanii*. It is possible that ssp. *greenmanii* diverged both morphologically (in floral and vegetative features) and ecologically as its ancestors migrated into the Gulf County region from adjacent northern areas, thus forming this cline-like series of intermediate populations. However, this variation pattern may have been produced through past hybridization and introgression between two previously isolated populations. In contrast, the extremely variable "hybrid" populations likely

result from a more recent spread of ssp. *filiformis* into this region following the construction of roads and highways (and the associated increase in disturbed, open, wet, grassy habitats). As *O. filiformis* ssp. *filiformis* spread into this region it encountered ssp. *greenmanii* (which is abundant in *Hypericum* bogs which can be found adjacent to highways). Both subspecies colonized the disturbed roadside habitats and interbreeding occurred. The fascinating variability of *Oxypolis filiformis* in the Florida panhandle thus may be explained through a combination of both primary (gradual geographical intergradation) and secondary (recent hybridization) factors (see Mayr, 1969).

Oxypolis filiformis ssp. *greenmanii* is one of several taxa endemic to various low-elevation habitats of the Florida panhandle, e.g., *Macbridea alba, Rudbeckia graminifolia, Hypericum lissophloeus,*

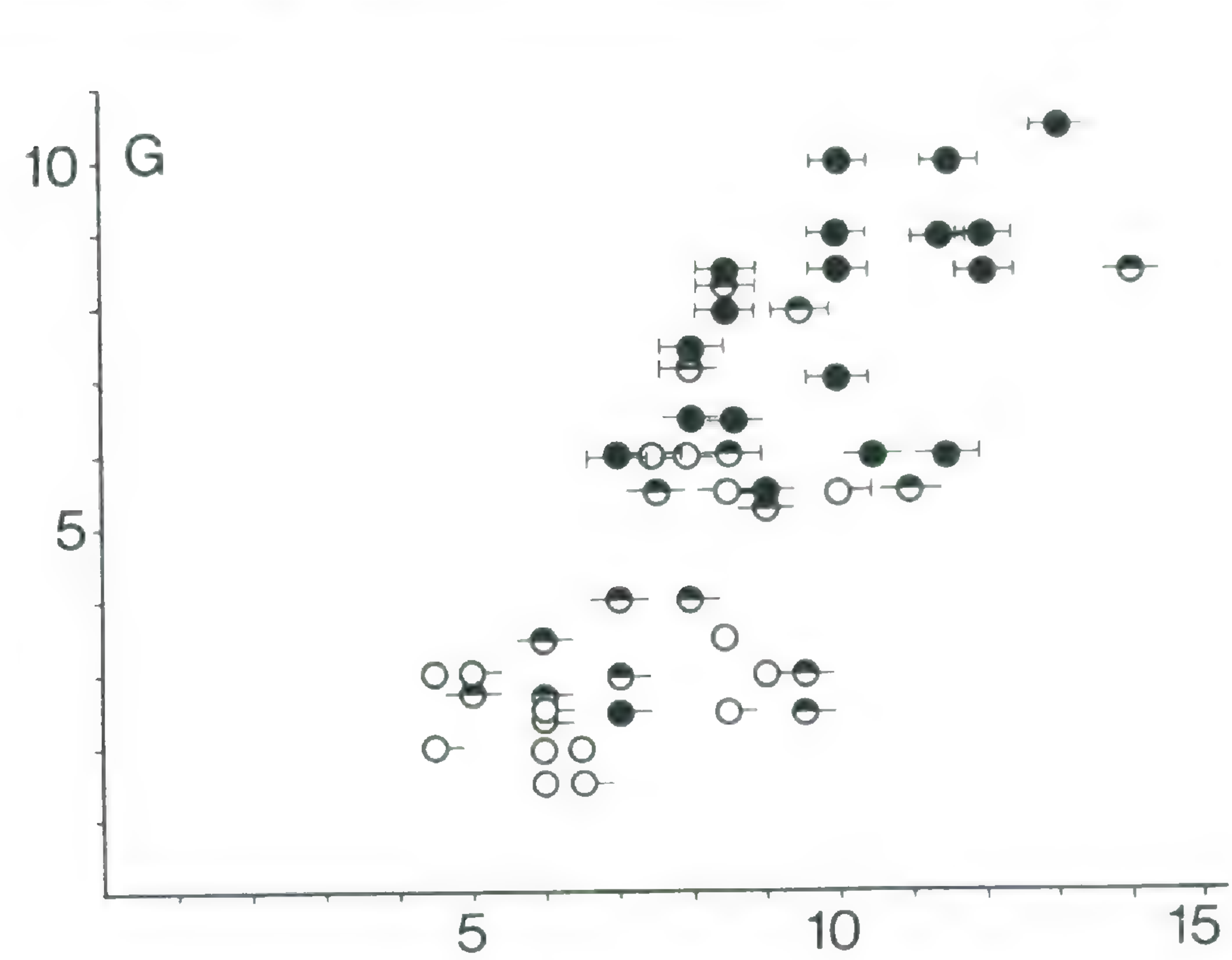

Figure 7. **Variation in certain morphological characters within population "G"—an extremely variable population consisting of Oxypolis filiformis, O. greenmanii and presumed hybrids.** Gulf Co., along Rt. 71, ca. 4 mi. S of jct. with Rt. 22 (S of Wewahitchka), in wet, disturbed roadside ditch, *Judd & Perkins 2749* (FLAS). See Figure 3 for explanation of symbols and graph axes.

Hypericum chapmanii, Gentiana pennelliana, Hedeoma graveolens, Liatris provincialis, Verbesina chapmanii, and *Xyris longisepala* (see also Ward, 1979). The causes of this area's high degree of endemism are poorly understood, but may eventually be clarified through systematic studies of the region's endemics.

ACKNOWLEDGMENTS

I thank Mr. Kent D. Perkins for his assistance during field studies in the Florida panhandle, and for his helpful comments and suggestions during the course of this study. Field studies were supported in part by a U. S. Fish and Wildlife Service Contract (No. 14-16-0004-79-100) for the investigation of endangered plant species.

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OCTOPLOID POPULATIONS OF OENOTHERA FRUTICOSA L. (ONAGRACEAE) FROM COASTAL NORTH CAROLINA[1]

GERALD B. STRALEY[1]

In 1818 Thomas Nuttall named *Oenothera riparia* from particularly robust specimens of a day-flowering *Oenothera* he had collected three years before on the banks of the Cape Fear River, near Wilmington, North Carolina (Nuttall, 1818). Since then a very few collections have been made of similar populations from coastal North and South Carolina, including the following representative material: North Carolina, New Hanover County, Wilmington, *Coville 189* (US), and *Biltmore Herb. 14944* (NY, US); South Carolina, Charleston County, Blake Marsh, *Alexander 53* (US).

Oenothera riparia has been variously treated in manuals since Nuttall named the species. Torrey and Gray (1840), Chapman (1860), and Pennell (1919) followed Nuttall in considering it a distinct species. Small (1933), in his Manual of the Southeastern Flora considered it a distinct species, although he had earlier (Small, 1896) considered it synonymous with *Kneiffia linearis* (Michx.) Spach (= *O. fruticosa* L.). Munz (1937, 1965) placed it as a subspecies of the variable *O. tetragona* Roth (= *O. fruticosa* ssp. *glauca* (Michx.) Straley). More recently, it has not been given taxonomic status, but rather considered a variant of the polymorphic *O. fruticosa* ssp. *fruticosa* (Radford et al., 1964; Straley, 1977). In a monograph of *Oenothera* sect. *Kneiffia,* I pointed out the characteristics of these populations and called for a cytological investigation of them (Straley, 1977, p. 400). At that time no recent herbarium specimens could be located, nor were any typical "*riparia*" populations found in the field during the study, although some populations with intermediate morphological characteristics between these robust forms and more typical *O. fruticosa* were collected. However, it was later learned that C. Ritchie Bell knew of "*riparia*" populations and in August 1979 David E. Boufford visited

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these localities. Boufford collected two populations of robust plants; along the NE Cape Fear River, Cowpen Landing, Pender County, North Carolina, *Boufford et al. 21575* (CM, MO), and 0.8 km S of Pender County line on Hwy. 421, New Hanover County, North Carolina, *Boufford et al. 21576* (CM, MO). Both populations were growing along the edges of the river and partially submerged in the river. Plants from these populations were grown at Missouri Botanical Garden, where they have been examined cytologically by Steven R. Seavey and Warren L. Wagner. Both populations were determined to be octoploids ($n = 28$). Meiotic associations were variable, with bivalents, and chains and or rings of up to eight chromosomes, as in octoploid populations of *O. pilosella* Raf. These are the first octoploid numbers reported for *O. fruticosa,* which is predominately tetraploid, with a few hexaploid popultions. As far as is known hexaploid populations are restricted to coastal areas, with a few in the Piedmont, from Virginia to northern Florida. Tetraploids are generally distributed throughout the range of the species, from Canada to northern Florida and west to Oklahoma. Furthermore, hexaploids are apparently restricted to the southern and lowland subspecies *fruticosa,* while the more northern and higher elevation subspecies *glauca* is strictly tetraploid. Chromosome numbers are known for no other coastal North Carolina populations, and for only one population, a hexaploid, from coastal South Carolina. The nearest known tetraploids to these octoploids are in coastal Virginia (Sussex, Prince George, and Dinwiddie counties), the Piedmont of North Carolina (Mecklenbergy County), and coastal Georgia (Jenkins and Tatnall counties).

The octoploid populations and similar populations of robust plants for which no chromosome numbers are known seem to be restricted to very wet situations on the Coast, often at least partially submerged. Some of the hexaploid populations not only exhibit intermediate morphological characters between the octoploids and the smaller tetraploids, but also grow in intermediate environmental conditions. They are often found in the edges of sluggish streams, as in a collection growing in the edge of the North Landing River, Virginia Beach, Virginia, *Straley 701* (MO, VPI). Typical *Oenothera fruticosa* from coastal areas is in more upland situations, often in sandy, well-drained soils.

Morphologically, the octoploid populations differ from most other coastal *Oenothera fruticosa* ssp. *fruticosa* in that the

octoploids are more robust, are much more branched, and generally more leafy throughout. Plants are less pubescent and the leaves are more succulent than most of the plants from drier habitats. Adventitious roots are prominent on the lower portion of the stems of progeny raised in cultivation, but were not apparent in nature, at least not on the voucher specimens collected. In size, plants are more like high elevation ssp. *glauca* populations, but the narrower leaves, non-glandular pubescence and shape of the capsules allows these robust plants to be placed readily with ssp. *fruticosa*.

The discovery of these octoploids indicates a need for further detailed cytological analysis of *Oenothera fruticosa* populations in coastal southeastern United States to determine the extent of octoploids and hexaploids and to detemine if there is any correlation between ploidy level and morphological characters or the semi-aquatic habitat. The octoploids must have arisen directly from tetraploids, but do the tetraploid populations still exist along the Coast?

Pending further investigation, I still see no benefit gained in giving taxonomic recognition to the hexaploid or octoploid populations, but rather recognizing them as a part of a highly variable species, morphologically, chromosomally, and in its habitat preference.

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A NEW CLEMATIS FROM NORTHEASTERN ALABAMA

ROBERT KRAL

In early May 1980, while collecting specimens from open and wooded lowlands along Dry Creek, south of the town of Ashville, St. Clair County, Alabama, I was startled by the bright blue of some tight clones of a "Viorna" type *Clematis,* these being rooted in a wet, sticky clay in highway right-of-way, but extending in some cases into adjacent swamp woodland. In addition to the striking density of the stems within clones there was the low but erect, definitely not viney, habit, the narrowness of leaf and the tendency of many shoots to produce but a single flower. Yet, though so many stems had but a single bloom, the overall effect of the clones was very showy because of their compactness. In digging some specimens from a patch I noticed that the stems indeed were interconnected by a branching system of deep-set pale brown rhizomes.

Comparison later of my material with that of *Clematis* at VDB likewise proved interesting in that, of the "Viorna," there are few that have bractless peduncles as did my specimens, and only one, *Clematis baldwinii* T. & G., combines this with an erect habit and flowers in the blue-purple range. Yet at the same time, were my plants to have a viney habit, their greatest affinities would be with the bractless-peduncled *C. crispa* L.

I returned to the locality on 16 May, again on 3 July, to sample fruit as well as to determine if the erect habit might not be merely an early stage or perhaps a result of cutting back of plants, in that most are in cleared area along a highway. However, it now appears that, throughout the season, the plants retain an erect, sparingly branched, tendril-less habit regardless of whether they are growing in cleared right-of-way or back in adjacent wooded border. Thus, while there definitely are resemblances to narrow-leaved extremes of the widespread *Clematis crispa,* there are strong distinctions, particularly in the development of rhizomes (a unique feature!), in stem habit, and in habit of flowering. These are set down in the following diagnosis and description:

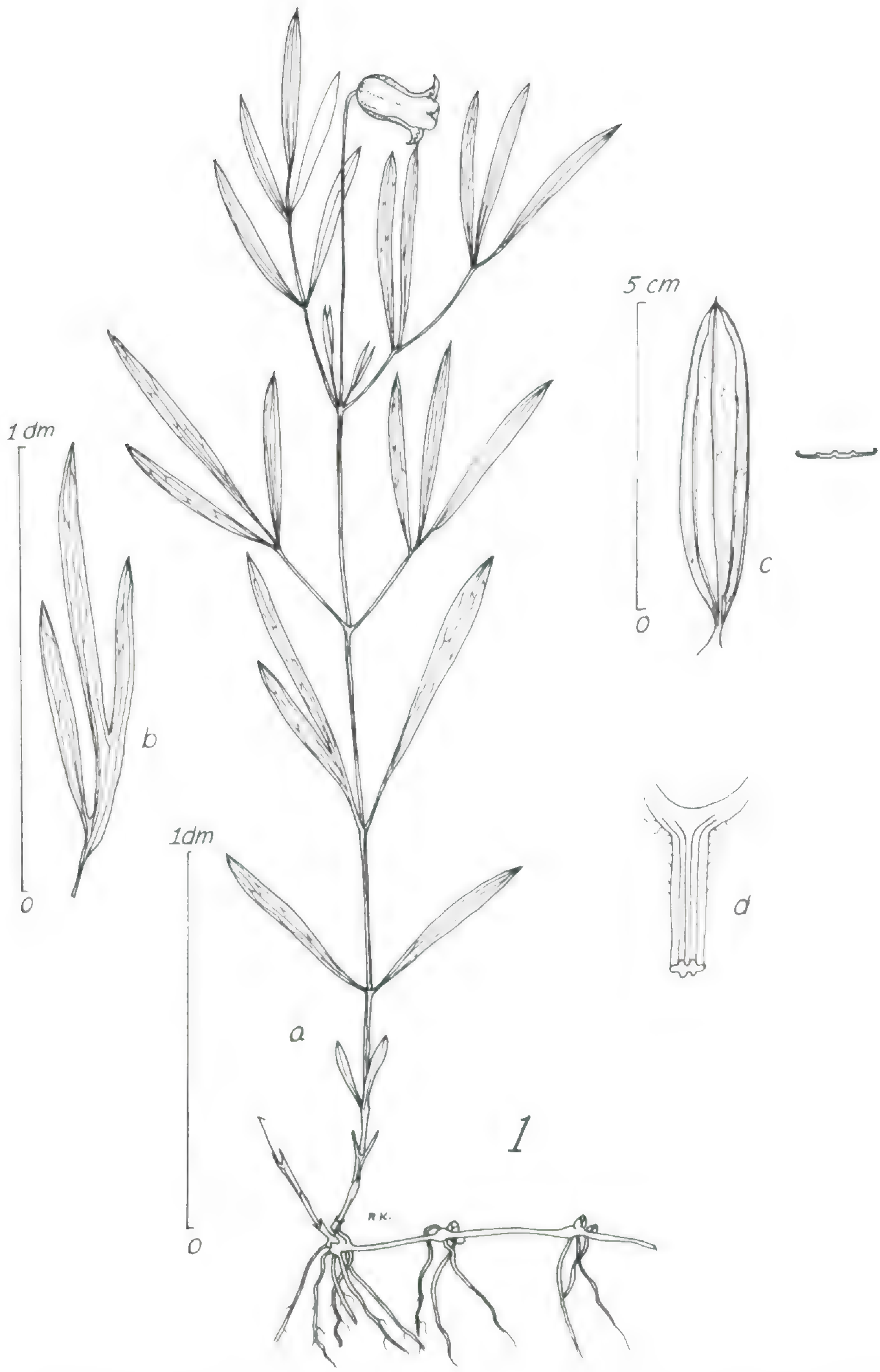

Fig. 1. *Clematis socialis*. **a.** habit sketch; **b.** cauline leaf extreme; **c.** leaflet, lower surface, cross-section; **d.** section of stem, node. From *Kral 64852*.

Clematis socialis Kral, *sp. nov.*

C. crispae L. affinis sed rhizomate, caulibus humilibus erectis vel ascendentibus, non scandentibus, foliis et foliolis angustioribus magis coriaceis, floribus solitariis vel paucis, notabilis.

Herbs superficially similar to *C. crispa* but forming dense clones by slender, horizontally spreading and branching rhizomes 2–3 mm thick. Stems erect or ascending from narrow erect caudices, solitary or in small clusters, simple or sparingly branched from penultimate nodes, mostly 2–3 (–5) dm high, the internodes several, the lowest shortest, 2–3 mm thick, the leafy ones longest, mostly 3–7, 1.5–2.0 mm thick, bright green or with purplish tints, glabrescent or with some persistent, pale villosity at and around nodes. Lowermost leaf pairs scale-like, oblong or triangular, mostly under 1 cm long, smooth; lower foliage leaves simple, sessile or short-petiolate, with blades mostly elliptic-linear, rarely spathulate, linear-lanceolate, or linear-oblanceolate (3–) 4–12 (–15) cm long, (0.3–) 0.5–1.0 (–1.5) cm wide, ascending or erect, with longer petioles at upper nodes, there becoming pedately trilobate with segments narrow as in simple blades, or pinnately compound, with petioles shorter than leaflets, arching-spreading or arching-ascending, the leaflets mostly 3–5, terminal longest, all shaped as in simple leaves, erect, somewhat secund, acute, mucronate, the mucro purplish, glandular, the margin entire, slightly revolute, the base narrowly acute or cuneate, both surfaces pale bright green, glabrescent or with sparse villosity along main veins beneath and on petiole and rachis, the main veins mostly 3 (to 7 in larger leaves or leaflets), strongly raised beneath, the pattern brochiodromous. Flowers urceolate to campanulate, spreading or nodding, solitary at tips of erect, slender, teretish, low-ribbed, variably elongated, purplish-tipped, smooth to apically villosulous peduncles. Sepals at anthesis lance-oblong or slightly panduriform, 2.0–2.5 (–3.0) cm long, apically spreading or recurved, acute to acuminate, thickest at the cupped base, the margin toward apex thin, dilated-crispate, medially and proximally entire, the convex backs pale but bright blue-violet, sparingly puberulent and strigillose, particularly on the 3–5 raised nerves, more densely so apically, white-villous-tomentulose marginally and on the apical petaloid dilation, the inner surface smoothish save at margin, proximally yellowish, faintly impressed-venose, distally blue-violet. Stamens yellowish, the outer ones slightly larger, all linear, 1.8–2.0 cm long, filaments 1.0–1.5 cm long, to 1 mm broad, pilose; anther

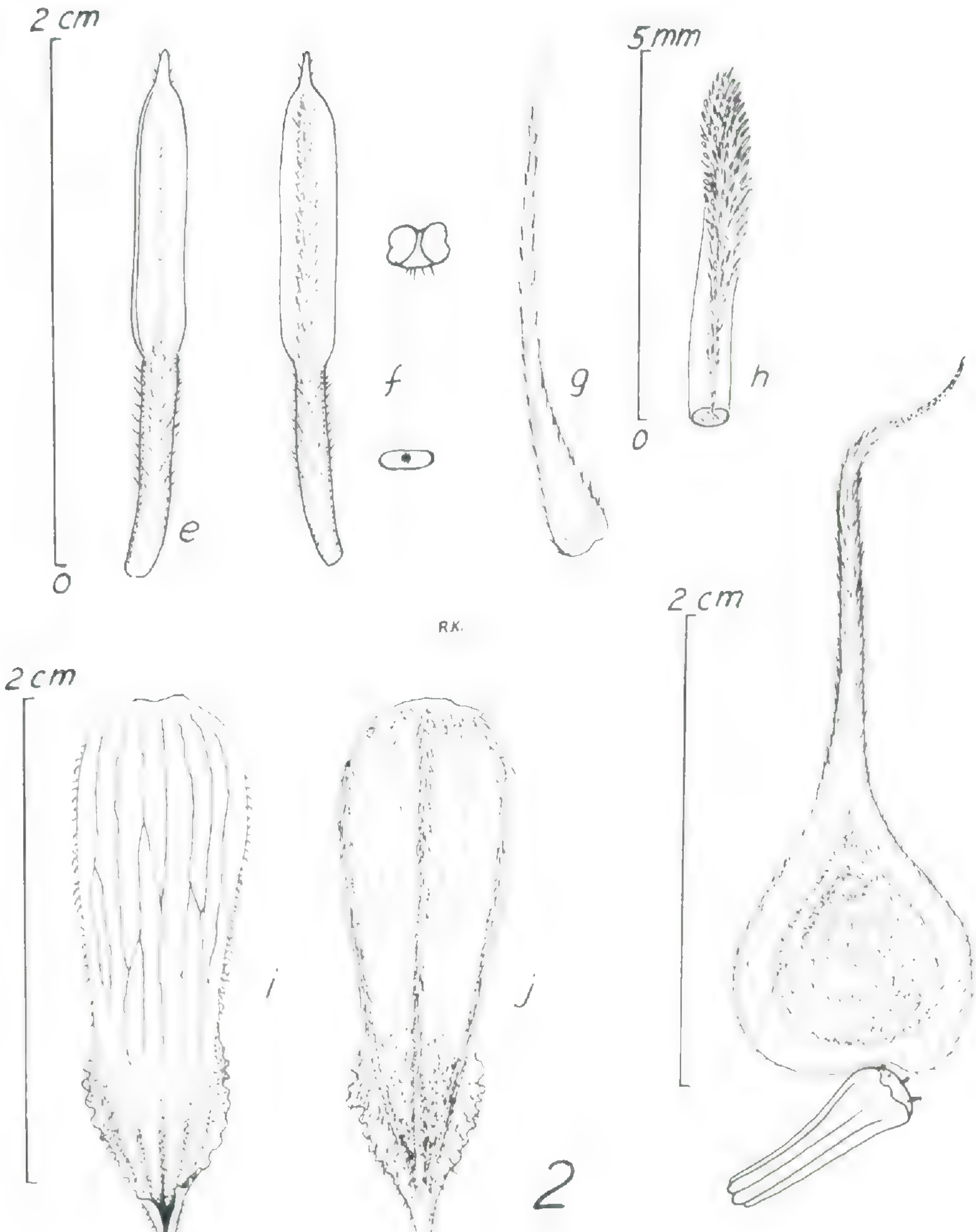

Fig. 2. *Clematis socialis*. **e.** posterior view of stamen; **f.** anterior view of stamen, cross section of filament, anther; **g.** young carpel; **h.** apex of style, stigmatic zone; **i.** inner side of sepal; **j.** external side of sepal. From *Kral 64852*. **k.** mature akene, apex of fruiting peduncle. From *Kral 65958*.

connectives pilose dorsally, apically apiculate. Carpels 1.2–1.5 cm long, the bodies lanceolate, tapering gradually into the elongate styles, the stigmas lineal, 4–5 mm long, smooth save for the bevelled, hairy ventral surface and stigma line, the surface otherwise concealed by a dense, silvery subappressed tomentum. Akene including style 2.5–3.0 cm long, the ovate body ca. 1 cm long, flattened over the seed, marginally spongy-thickened, wire-like, the apex acute, the surfaces appressed-strigillose-puberulous.

TYPE: ALABAMA. St. Clair Co.: silt and clay of alluvial, grass-sedge openings in bottoms of Dry Creek and contiguous hardwood-forested edges, ca. 3 mi. s. Ashville, 2 May 1980, *R. Kral 64852.* Holotype at US. Isotypes to be distributed. Additional material; 16 May 1980, *Kral 65108;* 3 July 1980, *Kral 65958.*

The lowland area immediately south of Ashville toward Beaver Creek Mountain is of considerable floristic interest, being characterized largely by numerous prairie-like openings, some of the more notable species in these being *Andropogon gerardi, A. scoparius, Panicum virgatum, Tripsacum dactyloides, Scirpus lineatus, Fimbristylis puberula,* many *Carex,* including the rather rare *C. meadii, Ranunculus fascicularis, Polygala sanguinea,* many Violets but particularly *V. pedata & V. sagittata, Asclepias viridis, A. hirtella, Phlox pilosa, P. amoena, Penstemon laevigatus,* etc., together with a wealth of composites including several common to southern and western prairie such as *Silphium terebinthinaceum, S. laciniatum, Liatris spicata & L. aspera.* The low areas from which the *Clematis* comes are grass-sedge dominated, some common species being *Eleocharis tenuis, E. compressa, Scirpus atrovirens, S. lineatus, Rhynchospora caduca, R. corniculata,* many carices, particularly *C. lurida, C. flaccosperma, C. tribuloides, C. squarrosa, C. granularis, C. debilis, C. festucacea, Glyceria striata, Poa, Juncus effusus, J. coriaceus, J. marginatus, J. filipendulus, Sisyrinchium atlanticum, S. langloisii,* and some common dicots being *Thalictrum, Ptilimnium costatum, Cicuta maculata, Phlox glaberrima, Penstemon laevigatus, Gratiola floridana,* etc. Surrounding forest, in the uplands is mostly pine-hardwood, the dominant pine being *P. taeda;* in the lowlands along the streams there are some cypress, but mostly mixed bottomland hardwoods, mainly willow oaks, southern hackberry, lowland hickory, and elms, with an understory principally of *Ilex decidua, Amorpha, Cornus.* There is considerable evidence of

logging disturbance, and of course some of the highway right-of-way had to be cut through wooded bottoms. However, there are sufficient prairie species in the area to convince the observer that some openings were present prior to white settlement. The soil has a high hydroperiod, is mostly a sticky admixture of silt, clay, and fine sand, probably circumneutral or slightly basic in the root zone of the *Clematis*. It is a good *C. crispa* habitat, though none of this species is in evidence.

While the relationships of *C. socialis* are plainly with *C. crispa*, and while Keener (1975) and others before him indicate a large number of segregates for this widespread species that ranges in low areas through the southeast save for Delaware, Maryland and West Virginia, it is difficult to place the "new" *Clematis* sensibly within *C. crispa* for the following reasons:

1. The stem habit is lower, erect, absolutely unvinelike, very comparable to that of *C. baldwinii*, a Floridean species that differs markedly in character of flower (larger, more purple) and fruit (larger, longer and plumose-tailed). No tendrils are produced.

2. Plants increase by means of spreading and forking rhizomes, the result being dense clones of sometimes hundreds of erect or erectish shoots. This would seem to be unique at least for *Clematis* of the southeastern USA.

3. Many plants produce but a single flower. Others may produce a pair of flowering shoots from the next node down, which very rarely may later rebranch and flower. The bractless peduncle is a *Clematis crispa* character; the flowering habit is not.

4. The leaves, in the context of other southeastern "Viorna" are narrower except in the case of extremes of *Clematis baldwinii* or *C. crispa* (var. *walteri* (Pursh) Gray). While the flower is much like that of *C. crispa*, it ranges smaller.

There is reason for some haste in publishing this note. So far I have seen this odd *Clematis* in but one small area totalling perhaps an acre, and most of this is along a U.S. highway, thus subject to the whim of the Highway Department. Contiguous private land in which the plant grows is being rapidly developed, mostly for housing. This means drainage and timbering, quite probably obliteration of the entire habitat in the near future. A careful check has so far revealed but six clones. It is thus reasonable that *C. socialis* qualifies as an endangered species, and that it be so nominated.

In 1981 an effort will be made to lift some specimens for purpose of propagation. Rearing some from seed and a subsequent study of the biology of *C. socialis* may reveal a better proof than is now available to me. It is a beautiful plant! The dense, low habit, the compact masses of bluish bloom set atop attractive foliage make it an excellent horticultural choice.

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CHEILANTHES PURPUSII (ADIANTACEAE), A NEW SPECIES FROM SAN LUIS POTÓSI, MEXICO

TIMOTHY REEVES[1]

A specimen filed as *Pellaea angustifolia* and bearing the annotation "*Cheilanthes* sp. nov." (GH) proves to be an undescribed species of *Cheilanthes*.

Cheilanthes purpusii T. Reeves, *sp. nov.* Figures 1 and 2.

A *C. hirsuta* Link stipitibus teretibus (non sulcatis) nigris, laminis planis, segmentis ultimis non pendulis, indusiis integris (non ciliatis), ad segmenta fere limitatis differt.

Rhizome short, stout, densely covered with concolorous sclerotic scales, these dark brown to black, linear-lanceolate, 2 to 4 mm long, ca. 0.3 mm wide at base, gradually to abruptly narrowed to elongate apex, falcate, often somewhat sinuous, entire or usually with small, blunt, tooth-like projections in upper ½ to ¼, sometimes the outer row of cells dark red-brown, slightly lighter than the dark central cells; stipe terete, glabrous (or with a few narrow deciduous scales like those of the rhizome), dark purple-brown, glossy, twice as long as blade, ca. 14 cm long, rachis deeply sulcate between rounded green wings, glossy, colored like stipe; blade deltoid to pentagonal, 7 to 8 cm long, 6 cm wide, herbaceous, dark green above, paler below, 3 to nearly 4 pinnate, glabrous above, minutely granular, with very few thick trichomes near margin (ca. 1 per 5 segments), pubescent below with minute trichomes (ca. 0.02 to 0.05 mm long), ultimate segments elliptic to oblong, 2 to 8 mm long, 1 to 2 mm wide, cuneate, rounded apically; indusium very conspicuous, highly modified, whitish, 0.3 to 0.5 mm wide, nearly entire with minute (ca. 0.02 mm) granulae or glands (?) which are mostly sessile or sometimes short-stalked, clearly distinct from leaf tissue, membranaceous, continuous around segment, slightly decurrent on axes, opaque, segment margin folded under, impressed with white spots marking vein endings at 1 mm intervals, these along line separating indusium from margin.

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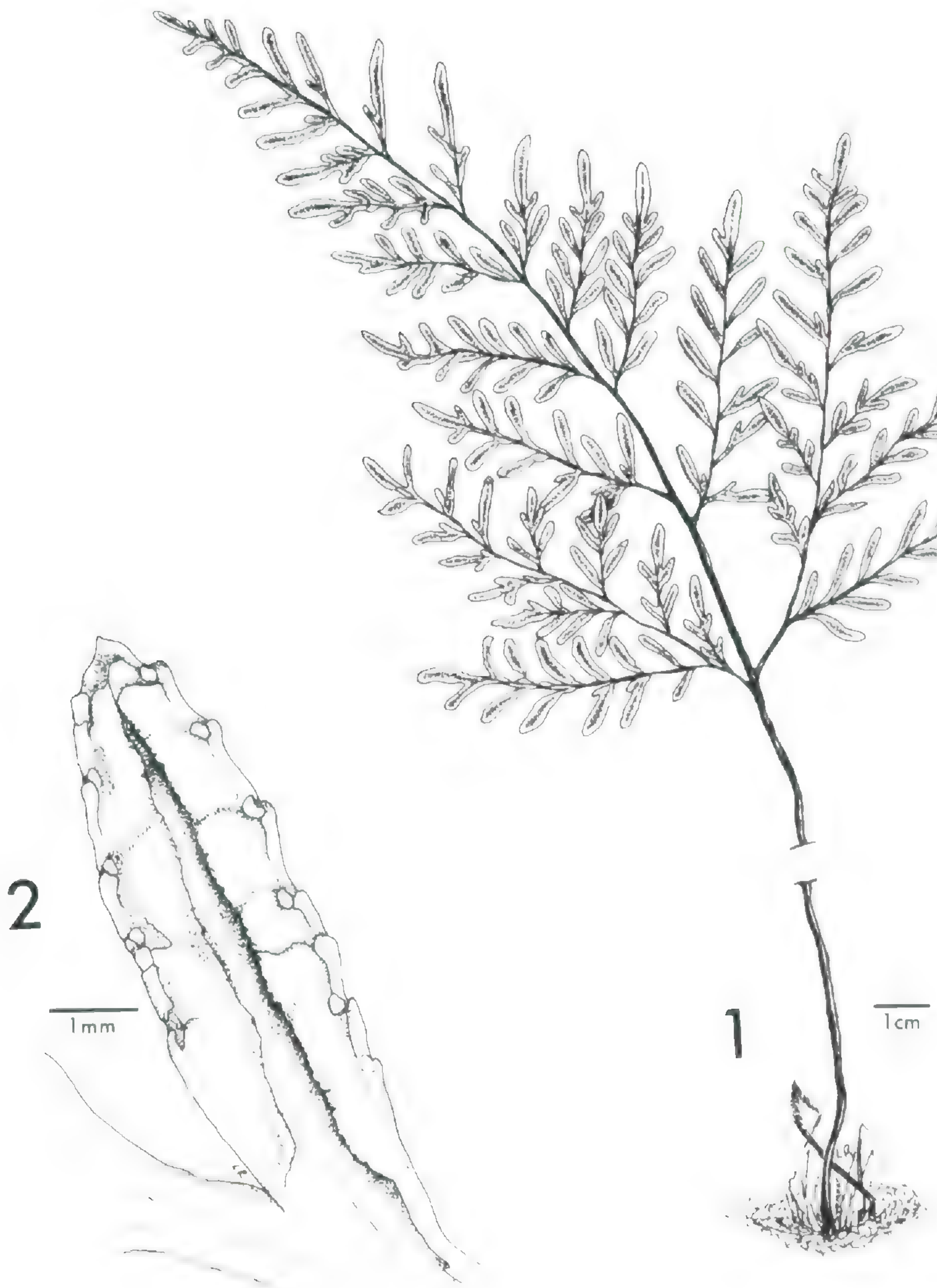

Figures 1 and 2. **Cheilanthes purpusii** T. Reeves, *sp. nov.* **1.** Habit. **2.** pinnule, lower surface. *Purpus 4881*, GH.

HOLOTYPE: Mexico: San Luis Potosi: Minas de San Rafael, *Purpus 4881* (GH!)

This species is related to *Cheilanthes hirsuta* Link, *C. marginata* HBK., and *C. arizonica* (Maxon) Mickel. It differs from these in its terete rather than sulcate stipe. There are no fracture lines in the stipe as are commonly found in these species and the broken stipes on the specimen are not "clean breaks" but are irregular. The stipes in *C. purpusii* are more slender and darker than in the other species, the rhizome scales are narrower and darker, and none of the others have minute or large trichomes on the under surface of the blade. The long-decurrent, ciliate indusia of *C. hirsuta* and *C. marginata* differ markedly from the very minutely glandular-margined, slightly decurrent indusia of the new species. *Cheilanthes arizonica* also differs in possessing dark red glandular dots on the lower surface of the blade.

Sousa (1969) locates Minas de San Rafael at 22° 13'N, 100° 16'W, placing it east-northeast of Ciudad San Luis Potosi in the southeast central portion of the state.

ACKNOWLEDGMENTS

I wish to thank the curators of the Gray Herbarium for the loan of the type material. I thank my wife, Linda, for preparing the illustrations.

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THE PROVINCELANDS GOLDEN CLUBS

RICHARD LEBLOND

The Golden Club (*Orontium aquaticum, Araceae*) is endemic to eastern North America and is at the northern limit of its range in Massachusetts (Britton, 1913; Fernald, 1950). This species is recognized as declining in abundance in Massachusetts and is considered to be endangered (Coddington & Field, 1978). There are but three extant stations for this species in the state, in contrast to ten known localities in the past (*ibid.*). The decline in abundance has been attributed to loss of habitat (*ibid.*).

The Golden Club ranges south from Massachusetts and New York to Florida, and west to Louisiana and Kentucky (Britton, 1913; Fernald, 1950). It prefers sandy, muddy or peaty shores and shallow water, bogs, and marshes (*ibid.*). The plant is a perennial, blooming in April and May (*ibid.*). The flowering stalk is the most distinctive feature of this beautiful aquatic plant, a white-stemmed, golden-tipped spear emerging a half-foot or more from the water's surface. A typical Golden Club plant will send up, radially, eight or more of these stalks.

Little is known of the natural history of this species, a deficiency noted by more than one of the authors cited. As example, a search of the literature uncovered only one reference to reproduction: "It is easily propagated by division of the rhizomes" (Raffill, 1946). Similarly, references to the ecology of the species are scarce.

OCCURENCE OBSERVATIONS IN THE PROVINCELANDS

Historically, Barnstable County Golden Club populations have been recorded in Truro (1890) and Yarmouth (1925) as well as in the Provincelands (1904, 1912, 1933) (New England Botanical Club Herbarium specimens). The Provincelands apparently contains the only surviving Cape Cod population. Murdoch, in his 1914 report on the Provincelands Golden Clubs in *Rhodora,* says "In four out of the six or seven ponds seen by the writer, *Orontium* is very abundant. Up to the middle of June it is the only conspicuous aquatic in these ponds." Hinds and Hathaway (1968) note that

"Several ponds in the Province Lands have quantities of this unusual plant."

This writer, after observing all of the more than thirty fresh water ponds in the Provincelands in 1980 and 1981, has identified eight separate Golden Club colonies. Five of the eight sites contained greater than one hundred individuals. In the three ponds with fewer numbers, one contained eleven individuals, another contained two, and the third, one. The ponds with populations of eleven and one are isolated from obvious human activity. The small population sizes may be due to such factors as water quality or age of the population. The pond with two specimens is discussed under "Threat Observations."

The predominant habitat of the Provincelands populations is shallow water with several inches of mud covering a sandy bottom. Although Golden Club is virtually the only aquatic in its immediate habitat during flowering (White Water-lily, *Nymphaea odorata*, emerges during the later stages in May), swamp and shoreline shrub communities and grass and cattail marshes grow in adjacent habitats. The Golden Club frequently intermingles at the border.

Only a few Golden Club plants were found growing away from standing water. However, in one area it is established forty feet from a pond on damp, needle-strewn soil in a Pitch Pine (*Pinus rigida*) woodland.

Following flowering, the Golden Club stalk begins to arch over until the inflorescence is completely under water during fruit production. Although this arching also occurred with Golden Clubs growing on land, such a reorientation of the inflorescence is probably related to the water, where the vast majority of the individuals grow. The water may afford protection for the developing seed, or contribute to successful seed dispersal. Consequently, water levels in these ponds may be critical for the preservation of the populations.

THREAT OBSERVATIONS

With one exception, all of the Golden Club populations occur wholely within the Cape Cod National Seashore boundary. One population is shared by the National Seashore and the municipality of Provincetown (the municipal portion is owned by the Massachusetts Division of Fisheries and Wildlife). The National Park Service has developed and maintained a variety of accesses and conveni-

ences for visitors to the Provincelands. These developments provide easy access to virtually every Golden Club colony. In spite of this access, human visitation has not obviously impacted any of the Golden Club populations. Individuals thrive at several access points, and fishermen were observed wading among the Golden Club plants in one pond. These access points lead off of developed trails, but are not in general part of the Park Service trail system, and are probably used by fishermen and hunters.

The greatest threat to Golden Club appears to be occurring in the pond adjacent to the Town of Provincetown municipal landfill (a dump until 1974) on land leased from the Park Service. The shore is a thick layer of mud and the surface of the pond is dark green with algae. The two Golden Club specimens in this pond produced only a few, undersized flowering stalks, and each withered before fruiting. The leaves did not develop above water on either plant, and by the end of May the plants had virtually disappeared from sight. These observations suggest this is a population in decline.

During April and the first week in May, the Golden Club populations were observed to be browsed by mature Canadian Geese (*Branta canadensis*). During this time, the shoreline was littered with Golden Club debris. No plant was observed to have lost all of its leafy shoots or flowering stalks, but the recovery of the affected plants was not monitored. The browsing was observed to cease after inflorescence maturation.

Fernald and Kinsey (1958) quote 18th century Swedish botanist Pehr Kalm as saying "the cattle, hogs and stags, are very fond of the leaves in spring." American Indians ate the roots and seeds, and called the plant *Tawkee* and *Tuckahoe* (*Ibid.;* Harris, 1968; Medsger, 1939). Wilson (1960) says "The *Araceae* as a group are notable for the occurrence of needle-like crystals of calcium oxalate (raphides) in 'packets' which occur in small capsules in almost all tissues. These account for the immunity of most *Araceae* to herbivorous mammals." It is possible these crystals develop in the Golden Club as the plant matures, thus allowing browsing during the early stages.

CONCLUSIONS

We do not know at present whether the Provincelands Golden Club populations are increasing, stable, or declining. There is evidence of at least minor habitat loss. Most existing populations

appear healthy and, by Massachusetts Golden Club standards, abundant. A detailed population survey is needed to monitor the health of the station.

The lack of biological and morphological data, especially regarding reproduction and dispersal, should be a major concern. Habitat needs, nutrient requirements, interaction between populations, pollinators, genetic variability, rhizome growth, and seed dispersal are all essential knowledge for successful management of these populations.

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NEW LOCATIONS FOR *PODOSTEMUM CERATOPHYLLUM* MICHX. (PODOSTEMACEAE) IN NEW HAMPSHIRE AND MAINE, WITH SOME COMMENTS ON A UNIQUE FLORAL FORM.

C. THOMAS PHILBRICK

Podostemum ceratophyllum Michx. (Riverweed) is a freshwater aquatic dicot that grows attached to rocks in rapids. This species is included on the New England regional rare and endangered plant list and was reported as rare in all the New England states but New Hampshire (Crow et al., 1981). However, I believe the lack of documentation of this plant in New England is a result of its being overlooked and subsequently undercollected. As noted earlier (Philbrick, 1981), possible reasons for this are the growth habit of the plant—which at a glance can be mistaken for an alga, and the often inaccessible habitat in which it grows.

During the summer of 1981 I visited numerous habitats in rivers in south-central New Hampshire and southern Maine in search of *Podostemum*. As a result of these visits I found the species growing in five rivers (eight additional towns) where it had not been previously reported. Additional sites, located in four towns, were also found in rivers already known to contain the plant.

In Maine *Podostemum* was found growing in four "new" rivers: the Sheepscot River, Lincoln Co. (Alna and several locations in Whitefield); Royal River, Cumberland Co. (Yarmouth); Androscoggin River, Cumberland Co.-Sagadahoc Co. line (Brunswick-Topsham line); and the Mousam River, York Co. (Kennebunk and Sanford).

I have thus far found one "new" river for *Podostemum ceratophyllum* in New Hampshire; the Ossippee River, Carroll Co. (Effingham-Freedom line). Mr. Peter Zika (pers. comm.) has recently collected the plant from the Connecticut River in Plainfield, Sullivan Co. This species is well documented from the Contoocook River in Boscawen, New Hampshire. I examined several rapid habitats upstream from Boscawen and found additional locations for the plant in Hopkinton and, as a result of

information supplied by Mr. Leslie Mehrhoff (pers. comm.), in Henniker. Both of these towns are in Merrimack Co.

The late Dr. Albion Hodgdon collected *Podostemum ceratophyllum* from the Lamprey River in Durham and Lee, New Hampshire. I found additional sites for the plant further upstream in this river in the towns of Epping and Raymond.

When flowers from the plants growing in the Mousam River, Kennebunk, Maine were examined, a previously unreported floral form was observed. The most striking difference between these flowers and those typically encountered was in the number of anthers per flower. Instead of the usual two or three anthers these possessed four, five, and sometimes six and seven anthers. A sample of 73 flowers was checked, of which 36 (49.4%) had four anthers, 28 (38.4%) had five, 5 (6.8%) six, and 2 (2.7%) had seven anthers. Only 2 flowers (2.7%) of the total sample had the usual two-anther complement. The stamen filaments in flowers of *Podostemum* are normally fused into a compound filament. In the case of these flowers, however, this compound filament is often twice the size of that normally found.

I also observed other floral appendages. One such appendage was green, somewhat resembling a leaf, but it seemed to arise from the lower part of the stamen filament and is very contorted in appearance. Another type is also green but is markedly flattened against the ovary and arises from its base. Anatomical and morphological investigations are currently underway to determine the nature of these unusual floral forms.

It is perhaps important to note here that many of the suitable habitats in the above mentioned rivers have yet to be visited and more locations for the plant probably will be found. For example, the Androscoggin River begins in northern New Hampshire and flows southeast across Maine, but *Podostemum* has only been collected far downstream in Brunswick, Maine. Suitable habitats no doubt occur in numerous other locations throughout the river.

Regeneration of plant fragments as a means of vegetative reproduction is known in *Podostemum ceratophyllum* (Hammond, 1936); the dispersal of these fragments may help to explain why the plant is often found in interconnected rivers. This information can also be used to find additional populations. For example, *Podostemum* is known from the Ossippee River in central New Hampshire.

This river flows east into Maine and empties into the Saco River in Cornish. As a result it is likely that new populations of the plant will be found in the Saco River, though as yet none are reported.

From these additions to the documented sites for *Podostemum* it is evident that the plant is not as rare as previously believed, at least in the region examined. I would like to suggest that it may be more significant to say that five additional *rivers* are now known to contain the plant rather than to specify only that 12 "new" towns were added to the distribution list. I suggest this because of the seemingly vulnerable nature of *Podostemum* populations to possible environmental impact (i.e., dam building and pollution). This is due to 1) the very specialized habitat in which the plant grows, and 2) the fact that all the populations located in a given river occur in a common aquatic "corridor." As a result of the latter fact all the populations in a river could conceivably be affected by a single point impact at some location upstream. This impact could then be transported downstream from population to population.

Therefore, I would like to suggest that, in the case of *Podostemum ceratophyllum,* individual rivers instead of towns be considered locations for the plant. This concept may also apply to other river aquatics, although it would not apply to all aquatics in general. Regardless of whether towns or rivers are considered as locations, the true distribution of *Podostemum* is not (and will not be) known until much more field work is completed throughout New England and elsewhere.

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ADDITIONAL RECORDS OF HICKORIES IN NORTHERN NEW ENGLAND

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Several records have turned up since my report of the distribution of *Carya* in northern New England (Rhodora **75**: 34 51, 1973).

Frank Seymour collected the shagbark and bitternut hickories in extreme northwestern Vermont, in South Hero, Grand Isle County. Specimens are in VT and NEBC. In a recent letter Dr. William H. Luginbuhl, Dean of the College of Medicine, the University of Vermont, told me that he had seen large trees of *Carya ovata* on rocky ridges in the town of Alburg, Grand Isle County, and in the town of Georgia, Franklin County. He observed a smaller tree, possibly planted, near the St. Albans-Swanton town line. He observed *C. cordiformis* in lower, wetter areas in the towns of Georgia and St. Albans in Franklin County. Dr. Luginbuhl has had extensive experience with hickories; he has planted several species on his property (pers. comm. in 1974 and 1981). Although he did not collect specimens on this special trip for me, there is no question as to the identity of the only two species of hickories known in northwestern Vermont, these two being easily recognized. The above records indicate that there is essentially a continuous distribution of these two species at lower elevations in western Vermont into southern Quebec. I have seen a number of specimens of shagbark and bitternut hickories from southern Quebec in the herbarium at Ottawa. The maps in my article in Rhodora and that in Little (U.S.D.A. Forest Service, Misc. Publ. No **1146**, 1971) indicate a break in the distribution in northwestern Vermont.

During the summer of 1980 Barry Levaas of Ascutney, Vermont, informed me of the presence of a very large number of shagbark hickories on the farm of Horace Putman, on Putnam Road, Springfield, Windsor County, Vermont: "a unique community, 700 or perhaps 1000 or more, in an area comprising not too many acres, common on fence rows and on a northeast facing slope where they grow with hemlocks, black birch, white pine and others. One tree cut down was tall and straight, free of knots for 20′ 30′ of its trunk, about 90 years old. The stand was cut over 30 or 40 years ago, but they regenerated themselves. North and south (of here) the trees are limited to a tree or two or a handful here and there." It is difficult to

explain the presence of this unusual colony. In August 1981 Horace Putnam brought me specimens of the shagbark hickory to verify the record; a specimen will be placed in NEBC.

Mr. Levaas brought to me in August 1980 a fruiting specimen of the hybrid hickory, *Carya laneyi,* from Hancock, Hillsboro County, New Hampshire. The leaves (5 7 leaflets) and fruits resemble those of the sweet pignut, *Carya ovalis,* but the nut shell is extremely thin (see also Rhodora **50**: 60 62, 1948); the meat is edible. A specimen is in NEBC.

Dr. H. K. Svenson reported to me in 1973 that *Carya ovata* occurs on rocks in Plympton, Middleboro, and Lakeville, Plymouth County, Massachusetts. In a letter dated May 18, 1978, Richard Champlin stated that *C. cordiformis* was found native in Foster and Cumberland, Providence County, Rhode Island, his first definite record from that state. He probably collected specimens.

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A SHORT-LIVED ADDITION TO THE FLORA OF CONNECTICUT

LESLIE J. MEHRHOFF

At the Annual Meeting of the Connecticut Botanical Society on 14 Nov. 1981, Mrs. Marie Pickhardt of the Society's Herbarium Committee asked for my opinion on her determination of a specimen of *Solidago*. She had collected the plant in Killingworth, Middlesex County, Connecticut on 24 September 1981. She noticed the population from which the plant came because, although it resembled a stand of *Solidago tenuifolia* Pursh growing nearby, there was a slight difference in the color of the vegetative parts of the plants. Mrs. Pickhardt had tentatively identified the specimen as *Solidago microcephala* (Greene) Bush. I agreed with this determination. According to Fernald (1950), *Solidago microcephala* differs from *Solidago tenuifolia* by having fewer flowers per head, mostly

pedicelled heads as opposed to glomerulate heads in *Solidago tenuifolia,* and by having a paler green color.

Mrs. Pickhardt's specimen appeared to be the first report of this species from Connecticut. According to Dowhan's Preliminary Checklist of the Vascular Flora of Connecticut (1979), *Solidago microcephala* has never been reported from the state. Seymour (1969) has no record of this species for New England. Fernald (1950), cites New Jersey as the northern limit of its distribution. Upon checking the G. Safford Torrey Herbarium at the University of Connecticut for further information I found a specimen of *Solidago tenuifolia* which had been collected in Groton, New London County, Connecticut on 7 September 1933 by K. P. Jansson. In 1976 when the late Harry E. Ahles was working on his Flora of New England he visited the G. Safford Torrey Herbarium and he annotated the Jansson specimen as *Solidago microcephala.* This appears to be the first collection of this taxon in Connecticut and possibly New England. Ahles also annotated a G. Safford Torrey collection of *S. tenuifolia* from Exeter, Washington County, Rhode Island, made on 11 September, 1948, as *Solidago microcephala.* Curators of other New England Herbaria should check collections of *S. tenuifolia* and *S. microcephala* to see if there are other records.

Sieren (1981) treats section *Euthamia* of the genus *Solidago* as a distinct genus, as it was first proposed by Thomas Nuttall in 1818. In his treatment *Solidago microcephala* is placed as a synonym of *Euthamia tenuifolia* (Pursh) Nuttall, without intraspecific rank.

If one accepts Sieren's treatment of the genus *Euthamia,* then *Solidago microcephala* is equivalent to *Euthamia tenuifolia.* If one accepts Fernald's treatment, it is a species of *Solidago.* Regardless of which author is followed, it is worthy of note that this morphologic form has been found in New England. This form should be looked for in other areas of the New England Coastal Plain. Additional localities should be noted in case further research on its status is warranted.

If the most recent treatment (Sieren, 1981) is followed, then what once was called *Solidago microcephala* no longer exists in Connecticut, or anywhere else for that matter. In light of the current interest in endangered species conservation, this may be a case of "Taxonomic Extinction."

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THE G. SAFFORD TORREY HERBARIUM AND
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PSILOCARYA SCIRPOIDES TORR., AN ADDITION TO THE CONNECTICUT FLORA

LESLIE J. MEHRHOFF

On 3 Sept. 1981 I noticed an unfamiliar sedge growing along the margin of Great Pond in Simsbury, Hartford County, Connecticut. I photographed the plant and took a specimen for later determination. While sitting out a rush-hour traffic jam near Hartford I decided to thumb through the sedges illustrated in Fassett's *A Manual of Aquatic Plants* (1969). The specimen that I had collected resembled the illustration of *Psilocarya*. I later found that the specimen matched those of *Psilocarya* at the G. S. Torrey Herbarium at the University of Connecticut. Upon closer examination, the long, beaked style of *Psilocarya scirpoides* Torr. was obvious.

On 27 Sept. 1981 I revisited the pond and found a large stand of this sedge approximatley 50 m from the first stand and growing in a similar habitat. Both stands were on the margin of the pond, which had been exposed by the late Summer low water level. I suspect that these areas are submerged in the Spring but are typically exposed at this time of the year. Other species growing in association with *Psilocarya scirpoides* were: *Cyperus dentatus, Dulichium arundi-*

naceum, Eleocharis obtusa, Eleocharis olivacea, Scirpus smithii, Scirpus torreyi, Eriocaulon septangulare, Juncus canadensis, Juncus pelocarpus, Rhexia virginica, Ludwigia palustris, and *Bidens frondosa.*

The genus *Psilocarya* is new to Connecticut flora. Fernald (1950) gives the range of this species as being from southeastern Massachusetts to eastern Maryland and to Michigan and northern Indiana. Seymour (1969) gives the distribution in New England as southeastern Massachusetts and Rhode Island, including a collection from Springfield, Massachusetts which is approximately 20 miles to the northeast of Great Pond. This area is frequented by many kinds of wading birds and waterfowl during the year. It is conceivable that the achenes were transported here from the Springfield locality by the birds, either internally or adhering to their feet. This species should be looked for in similar habitats in this region.

This is the first report of this taxon in Connecticut. As such, it should be considered as a rare plant in the state and will be added to the species which I am considering for inclusion in an update of Connecticut's rare vascular plants being prepared by the Connecticut Geological and Natural History Survey. *Psilocarya scirpoides* should be added to the list included in the Rare and Endangered Vascular Plant Species in Connecticut (Mehrhoff, 1978) with the significance codes RSTR and SCTS. Also, this species is included as a New England Endangered Threatened Species in Crow et al.'s list (1981) and an X should be added in the Connecticut column.

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THE G. SAFFORD TORREY HERBARIUM AND
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A NEW STATION OF GOODYERA OBLONGIFOLIA RAF. IN NORTHERN MAINE

L. M. Eastman, R. L. Hinkle, and D. M. Dumond

During botanical surveys conducted for the Superior Mining Company at T12 R8 WELS, Aroostook County, Maine, a new station of giant rattlesnake-plantain (*Goodyera oblongifolia* Raf.) was located. *Goodyera oblongifolia* is listed by the Critical Areas Program (1981) as being rare in Maine, the only northeastern state in which this plant occurs. Its first known discovery within the State was made by Kate Furbish in 1880 at Frenchville, Aroostook County; the following year she made collections from Madawaska and Fort Kent. Prior to the location of the T12 R8 station, it had been found at only ten locations in the state.

On July 20, 1981, a single non-flowering *Goodyera oblongifolia* Raf. was found in a dry wash area under mature sugar maple on an unnamed ridge south of Moose Pond. On July 22, 1981, a colony of approximately one thousand plants was found 1.7 kilometers to the south on a gently sloping, north facing terrace of Bald Mountain at about elevation 350 meters. The colony covers an area of about 0.4 hectare. About five percent of the population was in flower or budded. A dozen large plants were observed with reticulated leaves, suggesting hybridization with *G. tesselata* Lodd. However, reticulation is sometimes seen in plants from the far West where the latter species does not occur. The colony occurs under a dense canopy of mature (probably virgin) white cedar (*Thuja occidentalis* L.), red spruce (*Picea rubens* Sarg.), and balsam fir (*Abies balsamea* (L.) Mill.). An old growth stand of sugar maple (*Acer saccharum* Marsh) occurs at the edge of the site. The cedar, spruce, and fir range in size from 25 to 35.5 inches DBH and are estimated to be 100 to 450 years old. Many fallen logs in various stages of decay create an uneven microtopography. Inverted cones of accumulated

organic debris surround bases of most of the old growth white cedar present. Exposed roots of wind thrown trees exaggerate the soil-level micro-relief in many areas. Slopes adjacent to the terrace vary betwen 10 and 30 degrees. An intermittent stream enters the terrace from the south through a shallow cover. During dry weather the stream disappears under the terrace. During wet weather surface water and artesian groundwater is impounded up to several inches above the surface of the terrace. Such a hydrologic regime is responsible for the creation of the cedar-glade character of the habitat. The herbaceous species found in association include *Lycopodium lucidulum* Michx., *Botrychium virginianum* (L.) Sw., *Dryopteris spinulosa* (O.F. Muell) Watt, *Arisaema atrorubens* (Ait.) Raf., *Smilacina racemosa* (L.) Desf., *Goodyera tesselata* Lodd., *Mitella nuda* L., *Oxalis montana* Raf., *Viola renifolia* Gray, *V. septentrionalis* Greene., *Circaea alpina* L., *Aralia nudicaulis* L., *Cornus canadensis* L., *Moneses uniflora* (L.) Gray, *Pyrola elliptica* Nutt., *P. secunda* L., *Trientalis borealis* Raf., *Linnaea borealis* L. var. *americana* (Forbes) Reh., *Mitchella repens* L., *Galium asprellum* Michx., and *Prenanthes alba* L.

Additional searches for the orchid were conducted during August–October, 1981. As a result of these efforts, a number of additional sites where the plant occurs were located, most of which are on the slopes of Bald Mountain. These additional sites are generally located above the population found on July 22, 1981, on the north slope of Bald Mountain, as well as on the south slope of the mountain.

The most extensive population found outside the immediate vicinity of Bald Mountain occurs on the lower north slope of the ridge located immediately north of the mountain (locally called No Name Ridge). Several hundred plants may occur at this location, which is an ecotone between a poorly drained white cedar swamp and a spruce-fir/northern hardwood stand. A population was also located about 3.2 kilometers NNE of Bald Mountain near Carr Pond Mountain. These plants ocur along a drainage to Moose Pond Stream under a white cedar canopy.

The Bald Mountain station is significant due to the large number of orchids occuring there, as well as being about 55 kilometers south of any previously reported station in Maine. A specimen has been collected and will be deposited in the NEBC Herbarium.

Figure 1. *Goodyera oblongifolia* Raf. Bald Mountain, T12 R5 WELS, Aroostook Co., Maine.

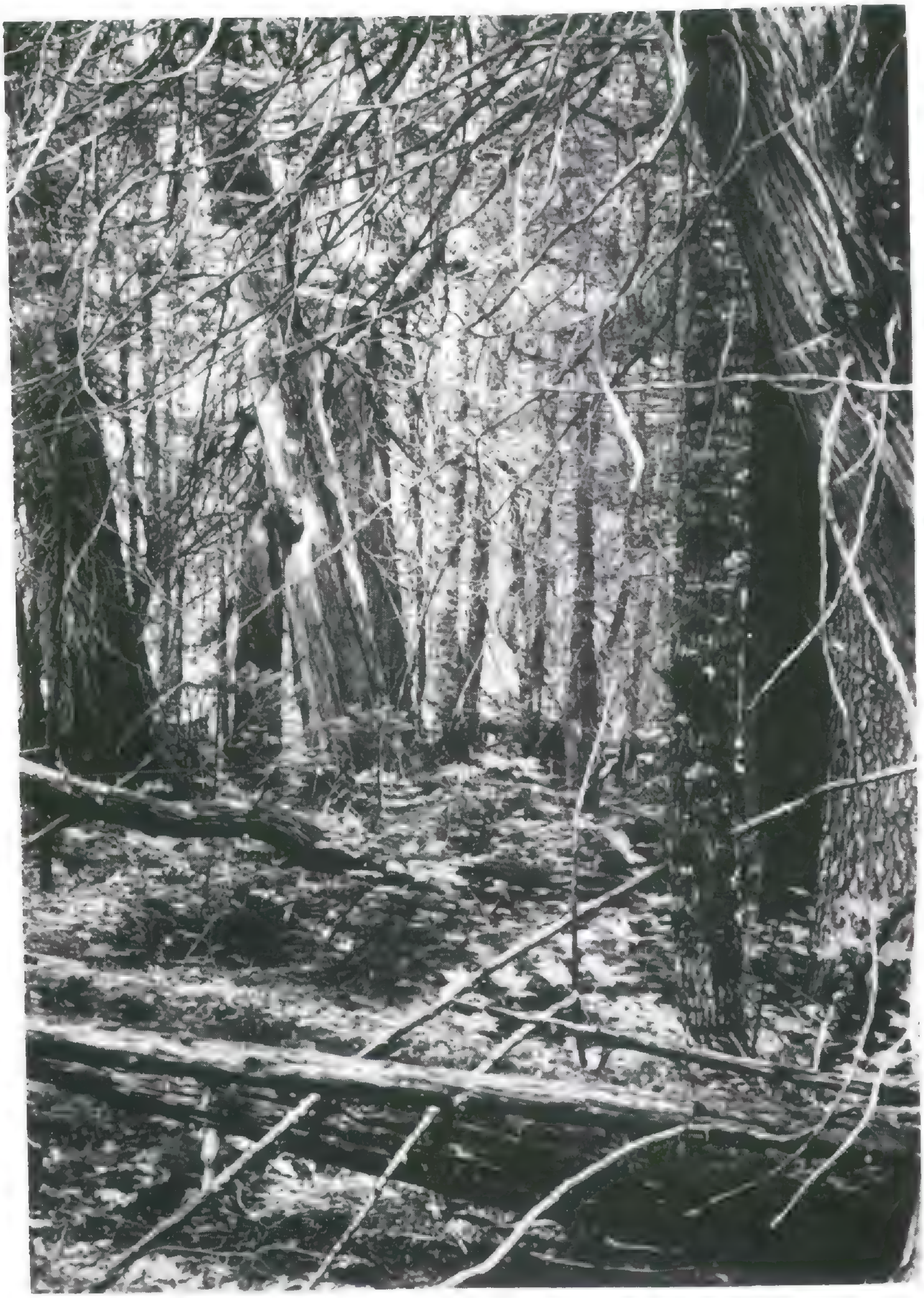

Figure 2. *Thuja* glade on Bald Mountain where *Goodyera oblongifolia* Raf. occurs.

Figure 3. Goodyera oblongifolia Raf. with reticulated leaves.

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BOOKS RECEIVED AND LITERATURE FOR NEW ENGLAND BOTANISTS

BORLAND, HAL. 1981. *A Countryman's Flowers.* xiii + 183 pp. Photographs by Les Line. Alfred A. Knopf, New York, N. Y. (Price $22.50)

The superb photographs of New England wild flowers, plus the knowledgeable and delightful essays about each, make this a lovely book to give or to own.

MILLER, W. REMINGTON. 1981. *Variations in Plankton.* xiii + 443 pp. Vantage Press, New York, N. Y. (Price $15.00).

This is a very technical book reporting the variations in plankton composition and density in the North Sea. Many diagrams and tables.

UPADHYAY, H. P. 1981. *A Monograph of Ceratocystis and Ceratocystiopsis.* xii + 176 pp. University of Georgia Press, Athens, Georgia. (Price $27.50)

Species of *Ceratocystis* are fungi of great economic importance which cause diseases of major crop plants such as sweet potatoes, sugar cane, coffee, and bananas. In the Northeast we see the results of the work of *C. ulmi,* in the Dutch Elm disease, and *C. fagacearum* which causes oak wilt.

FAHEY, TIMOTHY J. & WILLIAM A. REINERS. 1981. Fire in the forests of Maine and New Hampshire. Bull. Torrey Club **108**(3): 362–373.

The authors have made an extensive analysis of modern forest fires in Maine and New Hampshire in order to obtain a base on which to infer fire behavior in pre-settlement times, since there is a "mounting awareness of fire as a nearly pervasive environmental agent contributing to the evolution, structure, and function of terrestial ecosystems."

KINCAID, DWIGHT T. & ELIZABETH E. LYONS. 1981. Winter water relations of red spruce on Mount Monadnock, New Hampshire. Ecology **62**(5): 1155–1161.

The authors' observations do not fit previous generalizations. Their study provides data to consider in the quest for knowledge of

more of the factors determining "the causes, timing, and consequences of winter death of trees and their relationships to the position of timberline, than traditional winter desiccation concepts."

MARY M. WALKER
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Vol. 84, No. 837, including pages 1–157, was issued February 11, 1982.

Annual joint meeting of the
BOTANICAL SOCIETY OF AMERICA (NORTHEASTERN SECTION),
TORREY BOTANICAL CLUB, and PHILADELPHIA BOTANICAL CLUB
June 14, 15, & 16th

will be held at Framingham, Massachusetts, with the New England Wild Flower Society as host organization. Accommodations will be available at Framingham State College.

Field trips to Bartholomew's Cobble, Cape Cod, Concord, and Garden-in-the-Woods, Framingham are planned. An optional trip to the Arnold Arboretum on June 17th is also offered. Space is limited and advance registration is required. Full details may be had by writing the Chairman:

Mrs. Mary M. Walker
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The AIBS 33rd meeting

in conjunction with the Ecological Society, Fern Society, etc. will be held August 8–12th at Pennsylvania State University.

For further information, write:

AIBS Meetings Department
1401 Wilson Boulevard
Arlington, VA 22209

RHODORA April 1982 Vol. 84, No. 838

CONTENTS

A monograph of the genus Malvastrum A. Gray (Malvaceae:Malveae) II
Steven R. Hill. 159
The taxonomic status of Oxypolis greenmanii (Apiaceae)
Walter S. Judd 265
Octoploid populations of Oenothera fruticosa L. (Onagraceae) from coastal North Carolina
Gerald B. Straley 281
A new Clematis from Northeastern Alabama
Robert Kral 285
Cheilanthes purpusii (Adiantaceae), a new species from San Luis Potosi, Mexico
Timothy Reeves 293

NEW ENGLAND NOTES:

The Provincelands Goldenclubs
Richard LeBlond 297
New locations for Podostemum ceratophyllum Michx. (Podostemaceae) in New Hampshire and Maine, with some comments on a unique floral form
C. Thomas Philbrick 301
Additional records of Hickories in New England
Wayne E. Manning 304
A short-lived addition to the flora of Connecticut
Leslie J. Mehrhoff 305
Psilocarya scirpoides Torr., an addition to the Connecticut flora
Leslie J. Mehrhoff 307
A new station of Goodyera oblongifolia Raf. in Northern Maine
L. M. Eastman, R. L. Hinkle, and D. M. Dumond . . . 311
Books received and literature for New England botanists
Mary Walker 314
Notices of Meetings: BSA (Northeastern Section), AIBS 33rd inside back cover

Rhodora

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Cover illustration

Sagittaria cuneata, a northern species, is fairly common in northern New England, rarer to the South except down the Rockies. The species is variable, often producing flat, linear leaves similar to *Vallisneria americana* when growing submerged in rivers.

Original art by Pamela Bruns, reprinted here by permission from Hellquist, C. B., & Garrett E. Crow, *Aquatic Vascular Plants of New England. Part 3. Alismataceae,* New Hampshire Agr. Expt. Sta., UNH, Durham, N.H.

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JOURNAL OF THE
NEW ENGLAND BOTANICAL CLUB

Vol. 84 July 1982 No. 839

A MONOGRAPH OF THE GENUS MALVASTRUM - III[1]

STEVEN R. HILL

Section 6. *Malvastrum*

Malvastrum sectio **Malvastrum,** *emend.* S. R. Hill.

Carpella matura 9–16, indehiscentia vel dehiscentia margine proximali-apicale leviter, superficie apicale pilis simplicibus et pilis stellatis minutis, muris lateralis pericarpium crassis, ornata 2 cuspidibus distali-apicalibus 0.1–1.1 mm longis et cuspide unico medialiapicale 0.2–2.3 mm longo; marginibus pericarpium angulatis; endoglosso nullo; stamina 16–49, columnis staminalibus glabris; flores solitarii axillares vel in racemis terminalibus vel in racemis glomeratis axillaribus; bracteolis involucellis adnatis basi calyce vulgo; bracteae florales bifidae nullae vulgo vel praesentes; pilis caulinis stipitatis numquam; pollinis grana 15–32 aperturis. TYPUS: *Malvastrum wrightii* A. Gray [= *M. aurantiacum* (Scheele) Walpers].

The solitary axillary or racemose flowers, indehiscent or weakly dehiscent thick-walled tricuspidate mericarps, lack of an endoglossum, presence or absence of bifid floral bracts, glabrous filament tube, and 15–32 aperturate pollen characterize the section *Malvastrum*.

---

[1]This concludes the monograph. Parts I and II were published in the January and April issues of Volume 84 (1982).

12. **Malvastrum aurantiacum** (Scheele) Walpers, Annales **2**: 153. 1851. Fig. 60, 61.

Malva aurantiaca Scheele, Linnaea 21: 469. 1848. TYPE: **UNITED STATES.** Texas: black clay, moist prairie, Muskit (Mesquite) flats near New Braunfels, July, 1846. *F. Lindheimer 240* (distributed by A. Gray in Fascicle III under the number *350*) (LECTOTYPE: GH! (Berlin type lost); ISOTYPES: G!, GH!, GOET!, K!, MO!, NY!, OXF!, PH!, UC!, US!). *Malveopsis aurantiaca* (Scheele) O. Kuntze, Rev. Gen **1**: 72. 1891.

Malvastrum wrightii A. Gray, Mem. Amer. Acad. Arts n.s. **4**: 21, in adn. 1849. TYPE: **UNITED STATES.** Texas: *C. Wright s.n.* (LECTOTYPE: GH!; ISOTYPES; F!, NY!). *Sphaeralcea wrightii* sensu Metz, Catholic Univ. Amer. Biol. Ser. **16**: 142. 1934, non Gray, 1853.

Suffruticose perennial colonial herb 0.4 1.0 m tall from a woody caudex and an elongate thickened taproot that is pale salmon-red internally, with several sparsely branched lax and ascending main stems; *main stems* (2) 4 6 mm diam at base; *branches* when present 15 40 cm long; *vesture* of appressed (6) 8–10-rayed stellate-lepidote hairs 0.2 0.8 mm diam; *cotyledons* 12–18 mm long × 10 12 mm wide, ovate, apex retuse, base rounded, palmately 3-nerved; *stipules* (2) 4–6 (9) mm long × 1.0–1.5 mm wide, lanceolate, acute, somewhat falcate; *petioles* (5) 10 25 (45) mm long; *blades* (1) 1.7–2.2 (3)× longer than the petioles, (18) 30 40 (55) mm long × (10) 15 30 (45) mm wide, average midstem blade 1.4–1.6× longer than wide, ovate to wide-ovate, unlobed or very infrequently with two obscure lateral lobes half the distance from the rounded slightly cordate to truncate base, apex rounded, margin crenate-dentate with 1.5 3 teeth/cm, vesture of the adaxial surface of scattered appressed 6–8-rayed stellate to stellate-lepidote hairs 0.2–0.8 mm diam similar to those of the stem, abaxial pubescence dense with similar hairs: *flowers* soli-

---

Figure 60. **Malvastrum aurantiacum. a.** Habit, scale = 5 cm. **b.** Petal, scale = 2 mm. **c.** Stamens, styles and stigmas, scale = 2 mm. **d.–f.** Mericarp, lateral, distal, and apical views, scale = 1 mm. **g.** Mercarp, internal view, scale = 1 mm. **h.** Fruit, apical view, scale = 5 mm. **i.** Seed, apical and lateral views, scale = 1 mm. **j.** Calyx in bud, vesture of bracteole indicated, scale = 2 mm. **k.** Columella and carpocrater, scale – 0.5 mm. **l.** Stipule, abaxial surface, scale = 2 mm. **m.** Bracteole, scale = 2 mm. **n.** Midstem leaf, scale = 2 cm. **o.** Basal leaf, scale = 2 cm. **p.** Cotyledon, scale = 0.5 mm. **q.** Sub-lepidote (stellate-lepidote) hair, scale = 0.5 mm. (a,g-i, p from *Hill 6430;* b-c,j,l, from *Hill 5302,* d-f from *Lindheimer 240(350);* k from *hill 6112;* m,o,q from *Fryxell 1314;* n from *Fryxell 2947*).

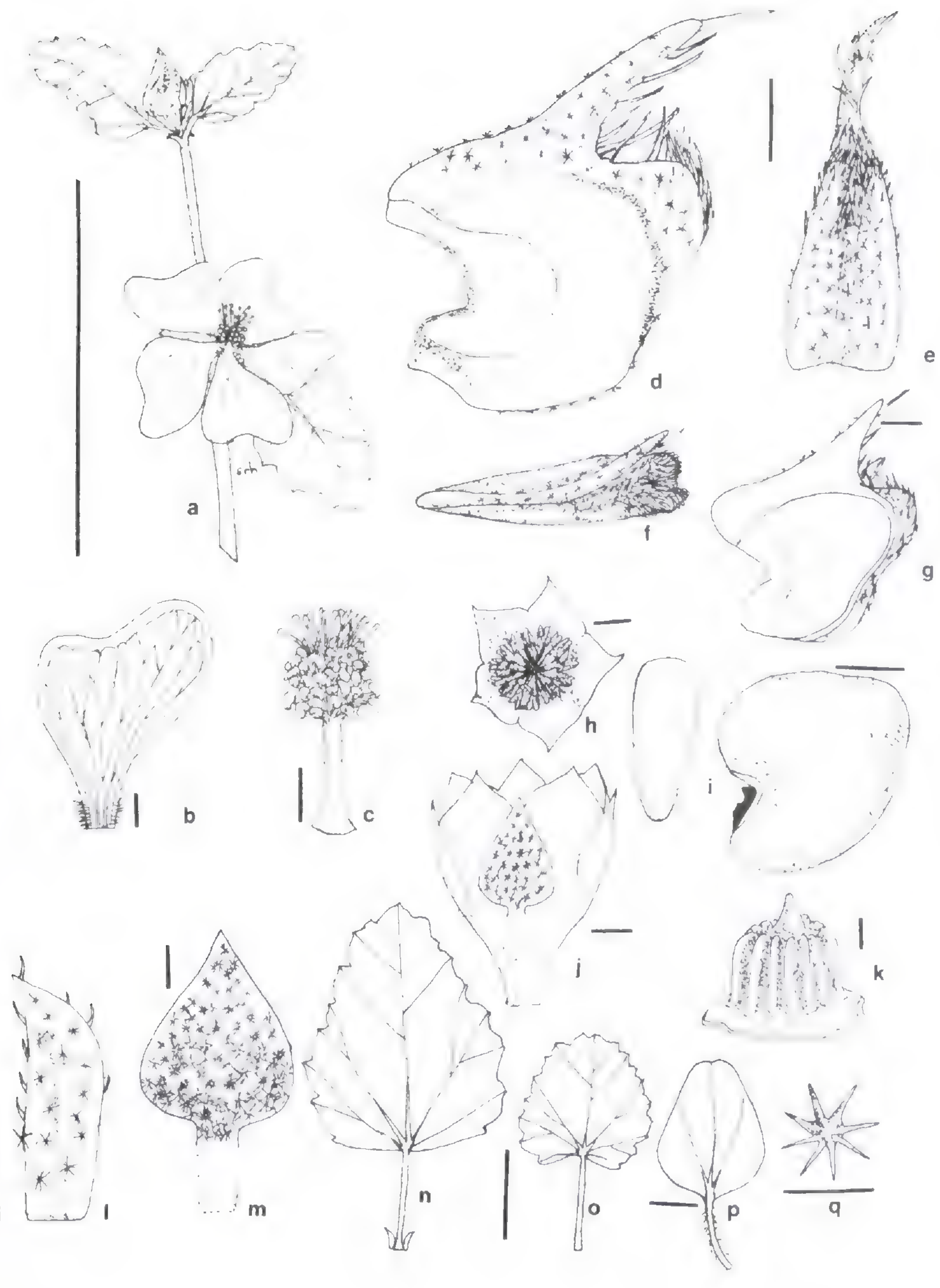
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Figure 61. **Malvastrum aurantiacum** (lectotype, GH).

tary in axils of well-developed leaves and stipules; *floral bracts* absent; *pedicels* 3.0–5.0 (10) mm long increasing by 2 mm in fruit; *involucel* of 3 bracteoles 8.0–9.0 (10.0) mm long × 3.0–5.0 mm wide, deltate-cordiform in the upper 4–6 mm and acute, abruptly narrowed and fused to the calyx in the lower 2–3 mm; *calyx* united 1/3 to 1/2 its length, 11–12 mm from pedicel to lobe apex, increasing to 13–17 mm in fruit, broadly campanulate, the lobes erect to slightly spreading, deltate, slightly auriculate at the base giving the bud a deeply angled appearance, acute to slightly acuminate, 7–8 mm long × 5–6.5 mm wide in flower to 9–10 mm long × 7–9 mm wide in fruit, vesture of the abaxial surface (similar to that of the bracteoles) scattered at apex becoming dense at base, adaxial surface of lobes downy pubescent in upper 2/3 and along the margins with minute simple arachnoid hairs; *corolla* golden-yellow to pale orange-yellow, petals conspicuously asymmetrically bilobed, (12) 15–16 mm long × 10–13 (15) mm wide, rotate at anthesis, exceeding calyx by 7–8 mm, claws densely pubescent on their margins with fine simple hairs 0.5–1.0 mm long; *androecium* with (28) 39–49 stamens, filament tube 4.0 mm long, glabrous, free portion of filaments 2.0 mm long, anthers 1.0 mm long × 0.8 mm wide after dehiscence; *gynoecium* with 12–16 loosely coherent carpels, style branching 4 mm above the columella, each branch terminated by a subglobose expanded stigma raised above the anthers 2.0–2.5 mm recurved at flower wilt, ovary surface densely pubescent with long rigid erect simple hairs 1–1.5 mm long; *schizocarps* 9–10 mm diam, raspberry-red and firm at first drying to tan or dark brown; *mericarps* (12) 14 (16), (4) 6 mm in height × (4) 5 (6) mm in length × 1.0–1.5 mm in width becoming slightly narrower apically, with a prominent distally directed medial-apical cusp 1.5–2.3 mm long, with two distal-apical contiguous flattened cusps 1.0–1.1 mm long, lateral surface unribbed, distal surface with an obscure medial line, vesture of both erect and appressed rigid simple hairs 1.0–1.2 mm long restricted to the distal surface of the apical cusps, with minute stellate hairs 0.1–0.2 mm diam throughout the upper third of the mericarp and along the distal surface, mericarp indehiscent, texture firm and woody, and proximal-apical region thin and solid, endoglossum lacking, readily separating from the receptacle at maturity; *seeds* 2.5–3.0 mm in height × 2.0–2.5 mm in length × 1.0–1.3 mm in width, considerably smaller than the mericarp chamber, with a slight bulge in the apical-distal region corresponding in position with the distal

cusps of the mericarp; *chromosome number:* $n = 18$, $2n = 36$; *pollen* 79.4–115.7 (99.7) μm diam, echinae (4) 7–10 μm, apertures 15 20.

Distribution. (Fig. 62). Restricted to heavy clay soils of river floodplains in the prairies of the eastern half of Texas, U.S.A., most frequent in the Coastal Bend region, from Cameron County in the south, north to Dallas and Tarrant Counties, west to the Balcones Escarpment, and east to Brazos and Jackson Counties, at elevations from sea level to 250 m.

Phenology and reproductive biology. Flowering from mid-May to mid-July, but periodically into early November during favorable wet warm periods. The flowers open 3 3:45 pm CST in the spring, early summer, and autumn and 1 2 hour later in mid-summer, closing at sunset (7 7:30 pm CST but occasionally remaining open until 8:30 pm CST). On cool, overcast days the flowers may open at noon. The stigmas are well-exserted until the flower wilts, at which time the styles recurve and the flower self-pollinates, allowing fruit formation in the absence of pollinators. Emasculated flowers did not set fruit. Field observations demonstrated that the flowers are visited by solitary bees (*Halictus ligatus*) and weevils (*Macrorhoptus sp.*) which gather or feed upon the pollen, respectively.

In greenhouse culture, seeds germinated in 17 30 days and the plants required 60–65 days of growth to the first flower. During the winter months, the plants remain dormant, blossoming again on vigorous new growth in the spring. Fruits were mature in 33–34 days after anthesis.

Discussion: Malvastrum aurantiacum is a Texas endemic whose origins are obscure. Its present distribution resembles the northern half of an Argentina-Paraguay, Gulf Coast disjunct distribution and suggests that it is a long distance disjunct whose ancestral South American population has disappeared. It appears most closely related to *Malvastrum coromandelianum*, particularly in its mericarp morphology (e.g. position of cusps), floral morphology, and ecology. This relationship is obscured by the higher ploidal level and quite different vesture and bracteoles.

As far as is known, the species does not occur south of the Rio Grande. This further supports the long-distance disjunction hypothesis over a south-north migration route.

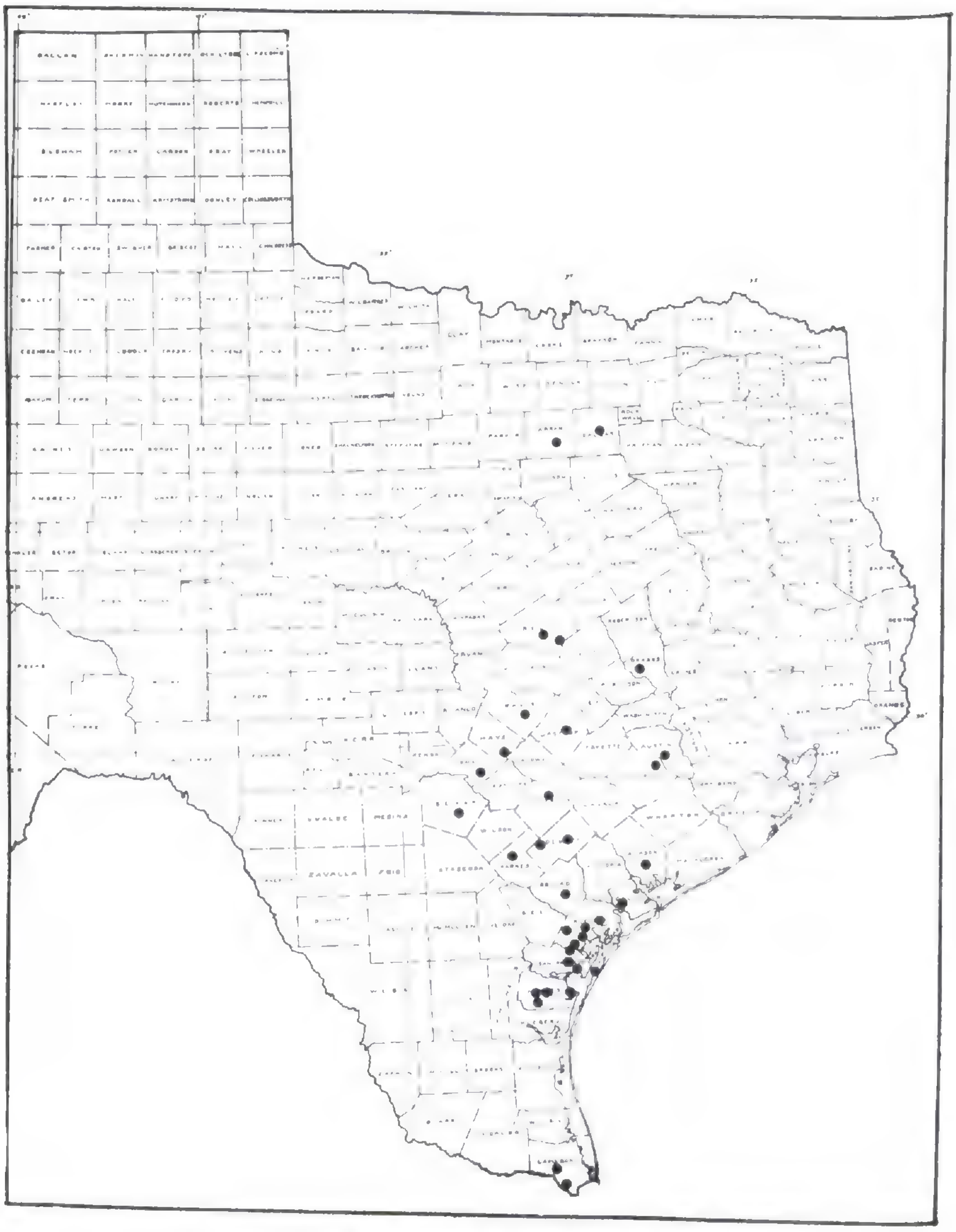

Figure 62. **Distribution of Malvastrum aurantiacum.**

SPECIMENS EXAMINED. **UNITED STATES.** TEXAS: Aransas Co., Aransas Pass, *Schulz 813* (US); Bastrop Co., Bastrop State Park, *Lynch s.n.* (TEX); Bell Co., Frio clay, 7 mi. SW of Temple, *Wolff 847* (TAES, US); Bexar Co., San Antonio, *Havard s.n.* (US); Brazos Co., banks of the Little Brazos River, Hwy. 21, 7 mi W of Bryan, *Hill 4514* (BRI, CTES, GH, srh, TEX) and *6430* (CTES, SMU, TEX): Calhoun Co., floodplain of Guadeloupe River near Hwy. 35, *Correll & Correll 38921* (FSU, GH, NCU, TEX, UC); Cameron Co., Brownsville, *Shiller M 102* (GH, MO, NY, TAES, US); Colorado Co., Hwy

71 just S of I-10 and Columbus, *Thomas et al. 39024* (NLV, pf); Comal Co., near New Braunfels, *Lindheimer 240* (=*350*) (G, GH, GOET, K, MO, NY, OXF, PH, UC, US); Dallas Co., clayey prairies, *Reverchon s.n.* (F, GH, NY, US, VT); lower Tarrant Rd., Grand Prairie, *Wenk 290B* (SMU); Dewitt Co., Cuero, *Tharp 2483* (TEX, US); Goliad Co., Cadena Creek near Hwy 239 crossing, O'Connor Ranch, ca. 5 mi. SE of Goliad, *Hill 5878* (SMU, US, VT, WIS); west bank of the San Antonio River, ca. 7 mi. SE of Goliad, *Hill 6112* (pf, TEX); Gonzales Co., Ottine, *Tharp s.n.* (TEX, US); Hays Co., San Marcos, *Stanfield s.n.* (NY); Jackson Co., Horseshoe Lake, near highway, *Drushel 10517* (MO, NY); Karnes Co., Panna Maria, Hwy. 123, near Jacobs Creek crossing, *Johnson 952* (TAFS, TEX); Nueces Co., Corpus Christi, *Parks & Cory 20654* (TAES); 3.5 mi. W of Petronila, *Fryxell 2947* (NY, pf, WIS); Refugio Co., west side of Melon Creek 1.8 mi. S of Hwy 774, *Hill 5302* (srh, TAES, US); along Sous Creek FM 1360, 1.1 mi. S of Woodsboro, *Hill 7231* (MO, NY); San Patricio Co., irrigation ditch, Hwy. 181, 2.1 mi NW of Gregory, *Hill 7639* (srh, VT, WIS); Tarrant Co., 6 mi, NE of Arlington, *Parks & Cory 32117* (TAES); Travis Co., Waller Creek, Austin, *Tharp s.n.* (MICH, TEX).

13a. **Malvastrum coromandelianum** (Linnaeus) Garcke subsp. **coromandelianum,** Bonplandia **5**: 295. 1857. Fig. 63, 64.

Malva coromandeliana Linnaeus, Sp. Pl. ed. 1, **2**: 687. 1753. TYPE: Hortus Upsaliensis, *Linnaeus* (LECTOTYPE: LINN 870.3). See discussion. *Malva coromandeliana* Panzer in Christmann et Panzer, Pflanzensyst. **8**: 448. 1782 ("*coromandelica*"). *Malva tricuspidata* R. Brown in Aiton f., Hort. Kew. ed. 2, **4**: 210. 1812. Based upon *Malva coromandeliana* L., and so a superfluous name. *Sida coromandeliana* Anonymous ex Schlechtendal et Chamisso, Linnaea **5**: 226. 1830, pro syn., a horticultural name cited as a synonym of *Malva tricuspidata*. *Malvastrum tricuspidatum* (R. Br. in Ait. f.) A. Gray, Pl. Wright. **1**: 16. 1852. *Malveopsis coromandeliana* (L.) Morong, Ann. New York Acad. Sci. **7**: 55. 1892. *Malveopsis coromandeliana* var. *α normalis* O. Kuntze, Rev. Gen. 3, **2**: 20. 1898, excl. specim. *Malvastrum tricuspidatum* var. *α normale* (O. Kuntze) Stuckert, Anales Soc. Ci. Argent. **114**: 28. 1932.

Sida jamaicensis Miller, Dict. ed. **8**: no. 5 under *Sida*. 1768, non Linnaeus, 1759. TYPE: Jamaica: Harbor. *Miller* (HOLOTYPE: BM).

Figure 63. **Malvastrum coromandelianum subsp. coromandelianum. a.** Flowering stem apex, scale = 2 cm. **b.** Petal, scale = 2 mm. **c.** Stamens, styles, and stigmas, scale = 2 mm. **d.-f.** Mericarp, lateral, distal, and apical views, scale = 1 mm. **g.** Mericarp, internal view, scale = 1 mm. **h.** Fruit, apical view, scale = 2 mm. **i.** Seed, scale = 1 mm. **j.** Calyx, scale = 2 mm. **k.** Columella and carpocrater, scale = 0.5 mm. **l.** Stipule, scale = 1 mm. **m.** Bracteole, scale = 1 mm. **n.** Midstem leaf, scale = 2 cm. **o.** Midstem leaf, scale = 2 cm. **p.** Cotyledon, scale = 5 mm. **q.** Vesture: 1) stem, 2) leaf, adaxial and abaxial surfaces, 3) calyx, 4) mericarp, scale = 0.5 mm. (a from progeny of *Fryxell 720a;* b-c, m from progeny of *Breedlove 20019;* d-f, h-i, k, q from progeny of *Percival s.n.;* g, j from progeny of *Board 1106a;* l from *Curtiss 6421;* n from *Hill 6053;* o from *Lloyd 1064;* p from progeny of *Hill 4579*).

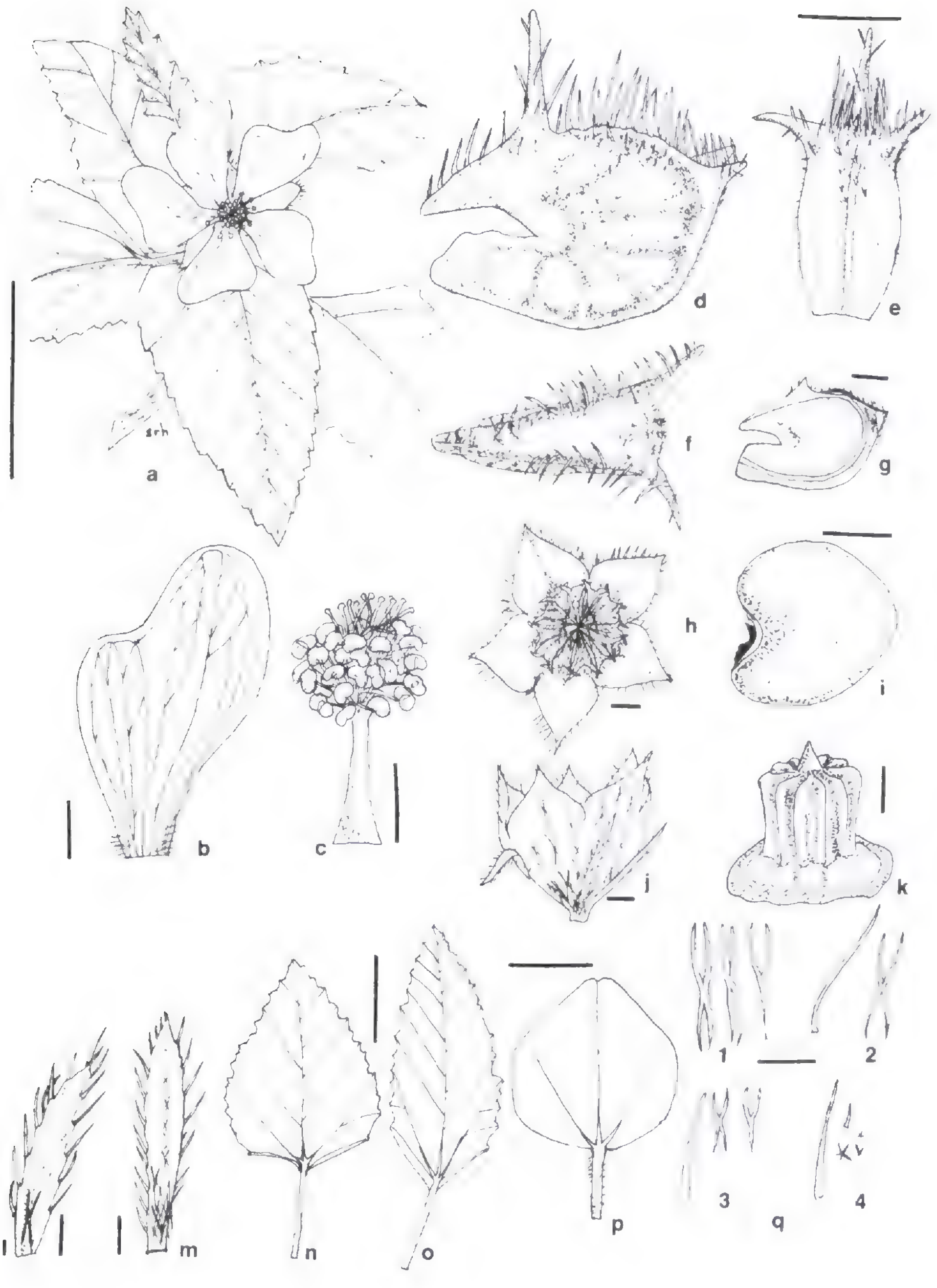
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Figure 64. **Malvastrum coromandelianum subsp. coromandelianum** (lectotype).

Malva subhastata Cavanilles, Diss. **2**: 72, t. 21, f. 3. 1768, pro parte. TYPE: Brazil. *Commerson s.n.* (LECTOTYPE: C!). See discussion.

Malva americana sensu Cavanilles, Diss. **2**: 80, t. 22, f. 2. 1786, non Linnaeus, 1753. Mistakenly applied to *Malvastrum coromandelianum,* as t. 22, f. 2 clearly indicates. *Malva americana* sensu Willdenow, Enum. Plant.: 729. 1809, pro parte, non Linnaeus, 1753. See discussion. *Malveopsis americana* sensu O. Kuntze, Rev. Gen. **1**: 72. 1891. *Sphaeralcea americana* sensu Metz, Catholic Univ. Amer. Biol. Ser. **16**: 142. 1934. All above excluding the basionym *Malva americana* Linnaeus.

?Malva europaea Noronha, Verh. Batav. Gen. **5**, art. 4: 20. 1790, nomen nudum.

Malva carpinifolia Desrousseaux in Lamarck, Encycl. 3: 754. 1792. TYPE: Description based upon "Alcea carpini folio Americana frutescens", Commelin, Hort. Amstel.: 3, t. 2. 1706 and on living plants of the Royal Botanical Gardens, Paris from America. No authentic specimens have been examined. Also cited in synonomy was Cavanilles, Diss. **2**: t. 22, f. 2. 1786, which is *Malvastrum coromandelianum.*

Malva hispida Moench, Meth.: 609. 1794, excl. syn. *Malva americana* L. TYPE: Moench's types have been lost, and since the description leaves no question as to its identity, it is chosen as lectotype. The description states "Pericarpia trirostrata, duo dorsalia, unum terminale" clearly indicating *M. coromandelianum.*

Malva antillarum Zuccagni, Centuria Prima: obs. 79. 1806. TYPE: based upon seeds sent by Thouin under the name "Malvae des Antilles". Zuccagni's types, formerly at FI, have been lost. The original description "foliis ovatis, obsolete trilobis, glabris, dentato-spinulosis, ciliatis; capsulis tridentatis, dentibus penicillatis" is chosen as lectotype. *Malva tricuspidata* R. Brown in Aiton var. *β subtriloba* De Candolle, Prodromus **1**: 430. 1824. Based upon *Malva antillarum* Zuccagni. A specimen in the Prodromus Herbarium (G-DC no. 430.1) is annotated with both names.

Malva domingensis Sprengel ex De Candolle, Prodromus **1**: 431. 1824. TYPE: Santo Domingo, 1820. *Bertero s.n.* (HOLOTYPE: TO; ISOTYPE: G-DC (microfiche no. 431.4), MO!, TO).

Sida carpinoides De Candolle, Prodromus **1**: 461. 1824. TYPE: Patr. ign., s. coll. *s.n.* (HOLOTYPE: G-DC)? There are no specimens in the Prodromus Herbarium microfiche bearing this name, which was based upon horticultural specimens of uncertain origin bearing the name *Sida carpinifolia.* The description, particularly "carpellis 10-11 dorso breviter bicornutis et basi interior 1-aristatis" indicates this species. Van Borssum-Waalkes (1966, p. 152) has apparently seen a specimen (G-DC) bearing this name, but did not comment upon it in detail.

Sida mucronulata De Candolle, Prodromus **1**: 461. 1824. TYPE: Java; s. coll. *s.n.* (HOLOTYPE: G-DC)? There are no specimens in the Prodromus Herbarium microfiche bearing this name, which was based upon specimens from Java similar to those of the preceeding but with more oblong-glabrate leaves and shorter cusps on the mericarp. However, van Borssum-Waalkes (1966, p. 152) refers to the holotype (G-DC) without comment.

Malva ruderalis Blume, Bijdr. Fl. Ned. Ind.: 64. 1825; non Salisbury, 1796. TYPE: Java: waste areas at Djakarta (Batavia), ?*Blume s.n.* (LECTOTYPE: L 908.137-216; ISOTYPE: P). The description "carpellis apice 1-cuspidatis supra basin 2-cuspidatis" along with its weedy nature clearly indicates *M. coromandelianum*. Van Borssum-Waalkes (1966, p. 152) has cited the types above. *Malvastrum ruderale* Hance ex Walpers, Annales **3**: 830. 1852. Presumably based upon *Malva ruderalis* Blume although this is not directly indicated, but is evidenced by the following statement "Planta Chinensis cum Javanica identica, testibus speciminibus *ab auctore* in utraque patria lectis" (italics mine) and the indication that the plant is native to Hong Kong and Batavia (Djakarta), Java.

Sida betulifolia Anonymous ex Schlechtendal, Linnaea **3**: 262. 1828, non Schrank, 1825, pro syn. A horticultural name cited as a synonym of *Malva tricuspidata* R. Brown in Aiton f.

Malva jamaicensis Anonymous ex Steudel, Nom. Bot. ed. 2, **2**: 94. 1841, pro syn. A horticultural name cited as a synonym of *Malva tricuspidata* R. Brown in Aiton f.

Malva tricuspidata R. Brown in Aiton f. var. *α microphylla* A. Richard in de la Sagra, Hist. Phys. Polit. Nat. Cuba. Bot.: 116, 1845. TYPE: no specimens cited, said to be frequent in cultivated areas of Cuba. Presumably based on small-leaved specimens of the typical subspecies, perhaps at P.

Malva luzonica Blanco, Fl. Fil. ed. **2**: 385. 1845. TYPE: Philippines: Luzon, Manila, *Merrill sp. Blanc. 451* (NEOTYPE: NY!; ISONEOTYPES: BO, L, P, US!) chosen by van Borssum-Waalkes (1966, p. 152). No type was indicated by Blanco. In Blanco, Fl Filip. ed. **3**: t. 251. 1879, this plant is clearly illustrated. No authentic specimens have been examined, and except for 400 specimens at MA, no Blanco collections are known.

Malva lindheimeriana Scheele, Linnaea **21**: 470. 1848. TYPE: United States . Texas: Comal County. Sterile places in dry, firm clay soil near New Braunfels, August, 1846. *F. Lindheimer 241* distributed by Asa Gray under the number *351* (LECTOTYPE: GOET! ISOTYPES: GH!, K!, MO!, OXF!, PH!, US!). The Göttingen specimen was annotated by Scheele. *Malvastrum lindheimerianum* (Scheele) Walpers, Annales **2**(1): 153. 1851.

Malvastrum carpinifolium A. Gray, Mem. Amer. Acad. Arts n.s. **4**: 22, in adn. 1849, quoad spec., excl. basionym. et syn. *Sida spiraefolia* Willd. et *S. planicaulis* Cavanilles. Gray incorrectly based this name upon *Sida carpinifolia* since he had in hand several misidentified specimens from Madeira, but cited as synonyms *Malva tricuspidata* Aiton and *Malva americana* Cavanilles.

Malveopsis coromandeliana (Linnaeus) Morong var. *β parvifolia* O. Kuntze, Rev. Gen. **3**(2): 21. 1898. TYPE: Paraguay. near Concepción, September, 1892. *O. Kuntze s.n.* (HOLOTYPE: NY!; ISOTYPE: US!).

Sida carpinifolia L.f. f. *umbrosa* Bornmüller ex Hochreutiner, Annuaire Conserv. Jard. Bot. Genève **6**: 33. 1902, nomen nudum, pro syn. Based upon a manuscript name on *Bornmüller 376,* Madeira (G!).

Sida carpinifolia L.f. f. *aprica* Bornmüller ex Hochreutiner, Annuaire Conserv. Jard. Bot. Genève 6: 33. 1902, nomen nudum, pro syn. Based upon a manuscript name on *Bornmüller 375,* Madeira (BR!, G!).

Malvastrum coromandelianum (Linnaeus) Garcke f. *breviaristata* Chodat et Hassler, Bull. Herb. Boissier ser. **2**(5): 290. 1905. TYPE: Paraguay. in saline fields near Concepción, September, 1902. *E. Hassler 7417* (HOLOTYPE: G!; ISOTYPES: BM!, G!, NY!, UC!). Despite the name, the types examined do not have conspicuously shorter cusps than usual for the species; the procumbent habit is a common adaptation seen in the species when growing under poor conditions, and the aspect of the plant as well as the locality matches that of f. *parvifolia* O. Kuntze. In a packet included with the holotype are several mericarps of a *Modiolastrum* that may have actually been the basis for the mericarp description.

Sida oahuensis A. Léveillé, Feddes Repert. Spec. Nov. Regni Veg. **10**: 120. 1912. TYPE: Hawaii. Oahu. Honolulu, April, 1909. *U. Faurie 839* (HOLOTYPE: presumably P; ISOTYPE: BM, G!, GH!).

Sida fauriei A. Léveillé, Feddes Repert, Spec. Nov. Regni Veg. **11**: 63. 1912. TYPE: Hawaii: Oahu, Waialua. *U. Faurie 5* (HOLOTYPE: presumably at P; ISOTYPE: BM).

Herbaceous annual or perennial 0.2–0.6 (−1.0) m tall but not infrequently flowering when only 6 cm in height, with ligneous crown and stem bases, with a single *main stem* (2) 3 5 (13) mm diam at base and with several to many erect to procumbent basal branches 30–60 cm and somewhat bushy, secondary branching infrequent and usually due to injury; stem *vesture* consisting of strongly appressed overlapping bilateral tardily shed 4-rayed stellate hairs 1.0–2.4 (3.0) mm long oriented longitudinally to the stem axis and usually with a swollen base, the rays infrequently connate or reduced to 2–3 (none simple); *cotyledons* (7) 9–10 mm long × (7) 9–10 mm wide, ovate, unlobed, minutely emarginate at the apex and truncate to broadly rounded at the base, petioles 5–7 mm long; *stipules* (2) 3–6 (8) mm long × 0.5–1.0 mm wide, subfalcate to falcate, lanceolate, acuminate, conspicuously ciliate on the margins with simple hairs 1.0–2.0 mm long borne on irregular marginal teeth; *petioles* (5) 10–20 (40) mm long; *blades* (1.5) 2.5–4.5 (7)× longer than the petioles, (17) 30–40 (65) mm long × (6) 15–30 (55) mm wide, usually not highly reduced towards apex, average blade 1.5–2.3× longer than wide, ovate to nearly lanceolate, unlobed or infrequently briefly 3-lobed halfway from the truncate to broadly rounded to frequently wide-cuneate base, apex acute, margin dentate to serrate with 3–5 (7) teeth/cm, vesture mostly on intercostal zones and basal part of veins, adaxial surface with scattered fine simple apically or marginally directed hairs or less frequently of 2–4-rayed bilateral stellate hairs 0.5–2.0 mm long, abaxial surface pubescent with simple and/or 2 4-rayed bilateral stellate hairs 1.0

mm diam, the former on intercostal zones and the latter on the veins; *flowers* solitary axillary, at full maturity occasionally congested at apices or rarely on reduced 2–3-flowered apical axillary branches and subtended by reduced leaves and stipules (one blossom produced/day/branch); bifid *floral bracts* lacking; *pedicels* 1–2 mm long in flower to 3–5 mm in fruit; *involucel* of 3 lanceolate, acuminate, subfalcate bracteoles 4–6 mm long × 0.6–1.0 mm wide, adnate to the calyx in the lower 0.5–1.0 mm; *calyx* united half its length, 5–7 mm in length and 8–11 mm in fruit, broadly campanulate, lobes spreading to incurved, deltate-cuspidate, 4–5 mm long × 2.0–2.5 mm wide to 5–6 (7) mm long × 5–6 mm wide in fruit, abaxial surface sparsely pubescent with primarily bilateral appressed (3)–4-rayed stellate hairs 0.5–1.2 mm long directed longitudinally along the veins, with a ciliate margin of simple hairs 0.7–1.2 mm long, adaxial surface nearly glabrous or with minute downy arachnoid hairs on the upper half and marginally to the sinus; *corolla* pale golden-yellow to orange-yellow, (15) 19–21 (24) mm diam at anthesis, petals asymmetrically bilobed, (6) 8–10 (13) mm long × (4.5) 6–7 (9) mm wide (often shrunken slightly in drying) rotate and planar, exceeding the calyx by 2–3 (5) mm, claws ciliate-pubescent at the basal margin with sparse tufted simple hairs 0.2–0.6 mm long; *androecium* with (16) 24–36 (40) stamens (tending towards 25) occasionally disposed in 5 rows, filament tube (1.5) 2–2.5 mm long, always glabrous, free portion of filaments (0.6) 0.8–1.0 mm long; *gynoecium* with (9) 10–14 (15) carpels, style branching 2 mm above the columella, each branch terminated by a conspicuously expanded hemispherical to subglobose stigma exserted beyond the anthers 1–2.5 mm but recurved at flower wilt; *schizocarps* (5.0) 6–7 mm diam including ornamentation; *mericarps* (9) 10–14 (15), (2.4) 3.0–3.5 (4.0) mm in height × (3.0) 3.5–4.0 mm long × 1.0–2.0 mm wide including ornamentation, with a single medial-apical cusp (0.5) 0.8–1.0 (2.0) mm long 1.0–1.2 mm distal to the proximal margin and with two divergent distal-apical cusps (0.3) 0.5–0.7 (1.0) mm long, lateral faces conspicuously ribbed especially at margin, vesture of the apical surface and cusps of firm proximally directed erect transparent simple hairs 0.6–1.0 mm long mixed with a few minute 2–5-rayed stellate or simple hairs ca. 0.05 mm diam, lateral and distal surfaces glabrous or with a few minute stellate or simple hairs at the apical margin or scattered over the distal 2/3 of the surface, the

proximal-apical chamber extension hollow, mericarp indehiscent or loosely sealed along the proximal-apical margin, endoglossum lacking, readily shed from the receptacle and calyx at maturity; *seeds* (1.5) 1.7–1.9 mm in height × 1.5–1.7 mm in length × 0.7–0.8 mm wide; *chromosome number*: $n = 12$, $2n = 24$; *pollen* 68 87 (108) (79) μm diam, echinae 5–8 μm, apertures (15) 20–32.

Distribution. (Fig. 65, 66) Pan-tropical in native or introduced populations mostly in alkaline soils between 35°N and 35°S latitudes; in the Western Hemisphere it is found from Texas and Florida in the north, south through the Caribbean region and Central America to coastal regions in South America to northeastern Argentina, not only in areas of human disturbance but also in river drainage systems at elevations from near sea-level to, less frequently, 2600 m.

Phenology and reproductive biology. In temperate portions of its range (such as Texas) plants begin flowering in mid-April and blossom continuously under proper conditions until frost in late November; in the frost-free portions of its range this species flowers all year with adequate water. Seeds from several populations cultivated in the greenhouse in Texas (i.e. *Board 1106a, Hill 4465, Hill 4579, Percival s.n., Fryxell 720a, Corral-L. 13, Breedlove 20019*, and *Morel 8095*) uniformly germinated 4 days after planting and flowered 50–60 days later at the 5th or 6th leaf node when 10 15 cm tall. Flowering was continuous as long as they were maintained, although they flowered less in the cooler winter months. Each flower, lasting a single day, opened at 3:45 4 pm CST and closed at 5:15–5:30 pm CST; flowers of the several populations from different regions raised together differed in this schedule by no more than 15 minutes. The stigmas, at first exserted beyond the anthers, began to recurve after one hour and were dusted by pollen.

Populations in Texas were observed frequently in the field throughout the year and at no time were pollinators observed on the flowers. Emasculated flowers did not set fruit. The plants seem to set fruit primarily through self-pollination, through the flowers are well-designed for cross-pollination and undoubtedly in some portions of its range the species often utilizes this mode. Fruits mature in 19–22 days from pollination.

As early as 1845, Blanco (Fl. Filip ed. **2**: 383) commented that the flowers of this species open at 2 pm and close at 4 pm. In Ghana,

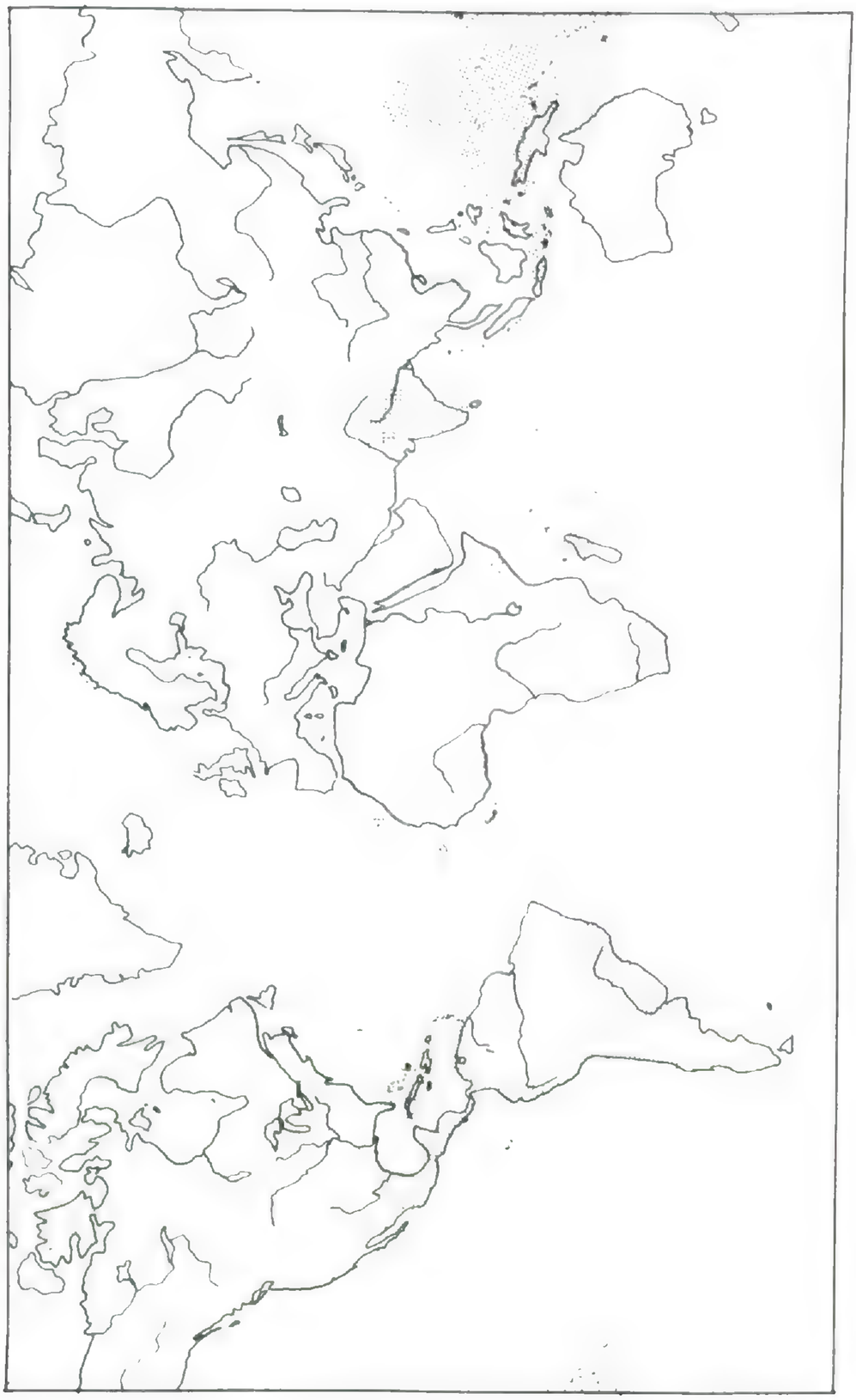


Figure 65. **Distribution of Malvastrum coromandelianum.**

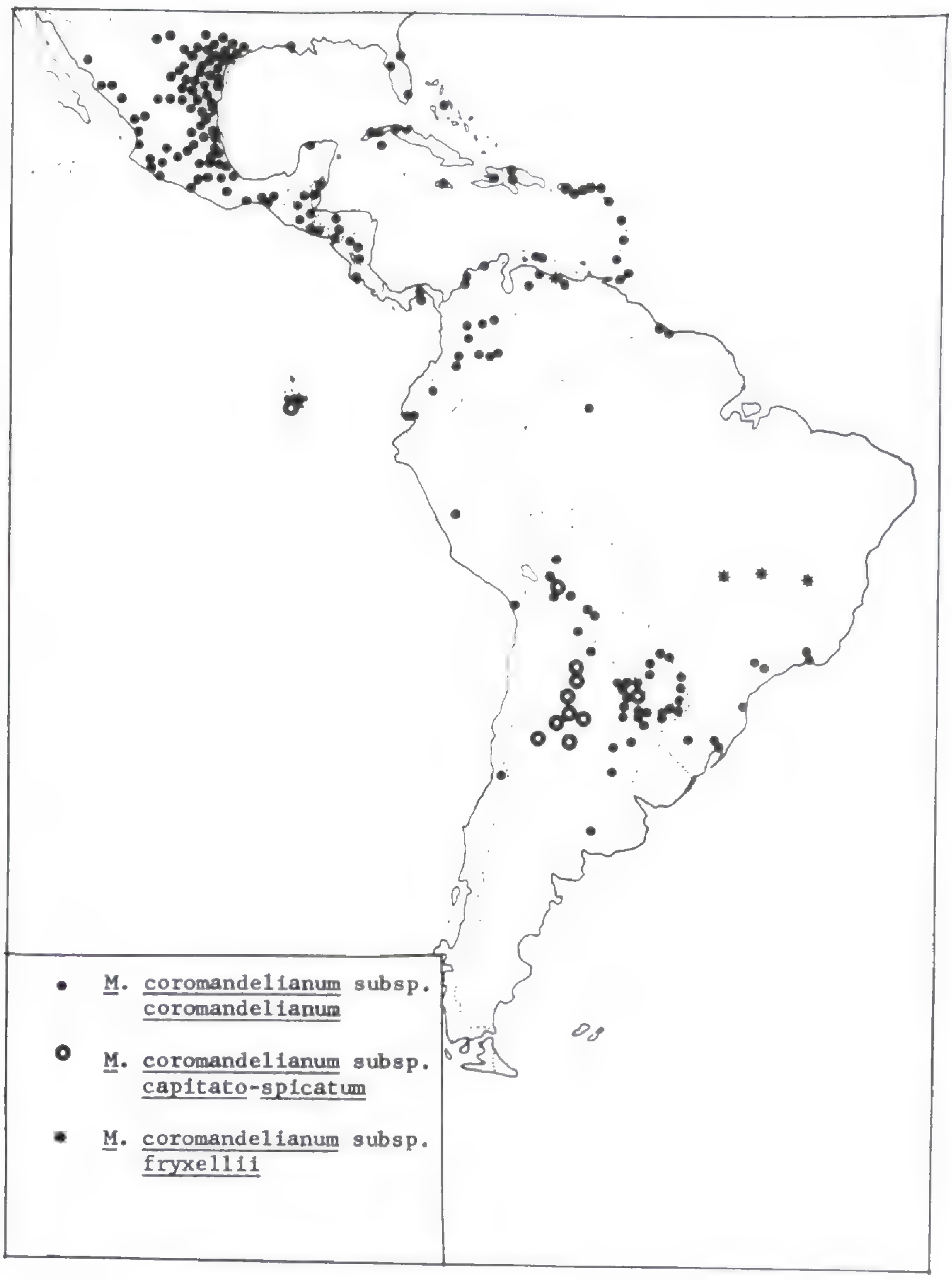


Figure 66. **Distribution of Malvastrum coromandelianum** in the New World.

the flowers are said to be open from 1:00–5:15 pm local time (Newton & Kisseadoo, 1978).

Discussion. The protologue of *Malva coromandeliana* Linnaeus contains several elements. Although Linnaeus cited as a synonym "Althaea coromandeliana, angustis praelongis foliis, semine bicorne" (Plukenet, Mantissa: 10, t. 334, f.2. 1700) as a basis of his name, this plate and description indicate *Sida acuta* Burm. f. The specimen in the Plukenet Herbarium (never examined by Linnaeus according to Stearn, 1957, p. 105) bearing this name (BM - photo Killip neg. no. 624 at US!) is composed of both *Sida acuta* Burm. f. and *Malvastrum coromandelianum*, the former matching Plukenet's plate. In the Clifford Herbarium (Linnaeus cited "Hort. Cliff. 346") is a specimen with two fragments (BM -Killip neg. no. 623-US!) one of which is this species but the annotations are in a hand other than that of Linnaeus. In the Linnaean Herbarium are several specimens, one of which (LINN 870.3) is annotated "H.U., *Malva* 2 *coromandeliana*" in Linnaeus' script. Since this specimen is part of the protologue (Linnaeus cited "Hort. ups. 201") and since it is a representative specimen, it has been designated as the lectotype.

Malva subhastata Cavanilles was based on an assemblage of vegetatively similar specimens from such diverse regions as Brazil, Peru, and Réunion. His figure (t. 21, f.3) depicts *Malvastrum coromandelianum* with regard to such features as the lanceolate stipules and ciliate calyx. Cavanilles cited "Ex itineribus Commersonis . . . v.s. communicatam a D. Thouin". The specimen at Copenhagen bears the label "Malva foliis angulatis; *Commerson:* e Brasilia ded. Dr. Thouin" and is chosen as the lectotype. *Malvastrum coromandelianum* occasionally has briefly three-lobed leaves (the lobes in the lower half of the leaf) that may by some be termed subhastate.

Willdenow misapplied the name *Malva americana* to *Malvastrum coromandelianum*. In the Willdenow herbarium are four specimens bearing this name, all no. *12751* (B-W). The first two sheets are *M. coromandelianum*, the third is probably *M. corchorifolium*, and the fourth is tentatively assigned to *M. coromandelianum*.

When one thinks of the genus *Malvastrum*, the most frequent species *Malvastrum coromandelianum* first comes to mind. The species is easily identified by means of its tricuspidate mericarps and weedy habit. In the Caribbean and Central America, *M. coromandelianum* can be distinguished from *M. corchorifolium* by the

indument of simple hairs on the upper leaf surface of the former. The species establishes itself readily throughout the tropics, and is particularly well-established in India and Polynesia. However, there are few specimens from Africa and the majority of Australia. *Malvastrum coromandelianum* subsp. *coromandelianum* is most diverse in the Paraná region of Argentina and Paraguay, and again from Texas to Mexico, particularly regarding flower size, position, hue, and plant habit. Introgression may be occurring with subsp. *capitato-spicatum* in Argentina.

REPRESENTATIVE SPECIMENS: **UNITED STATES.** MASSACHUSETTS: Middlesex Co., wool waste dump, Westford, *Fletcher s.n.* (GH, US); PENNSYLVANIA: Delaware Co., wharves and railroad sidings, Chester, *Benner s.n.* (PH); Philadelphia Co., introduced at Old Navy Yard, Philadelphia, *Burk s.n.* (F, PENN); NEW JERSEY: Camden Co., on ballast, Camden, *Martindale s.n.* (F, MO, NY, PH, US); FLORIDA: Dade Co., Homestead, *Gillis 7281* (BH, MO); Leon Co., Tallahassee, *Godfrey 53354* (FSU, GA, GH, NCU, NY, SMU, UC); St. Johns Co., St. Augustine, *Curtiss 6421* (BKL, CU, DAO, G, GH, MO, NY, UC, US, VT); ALABAMA: Mobile Co., Mobile and Ohio RR wharf, Mobile, *Mohr s.n.* (US); LOUISIANA: Cameron Parish, Hwy. 82 E of Grand Chenier, *Thieret & Reese 9997* (DAO, FSU, TEX); TEXAS: Bastrop Co., Bastrop, *Duval s.n.* (TEX, US); Bexar Co., San Antonio, *Albers 44008* (SMU, TEX); Brazoria Co., Columbia, *Bush 303* (GH, MO, NY, UC); Burleson Co., 5.5 mi. N of Snook, *Hill 4465* (srh); Calhoun Co., Port Lavaca, *Tharp 1585* (NY, TEX); Callahan Co., Baird, *Letterman 101* (MO); Cameron Co., 4 mi SE of Olmito, *Hill 6053* (TEX); 1 mi. W of Palmito Hill, Rte. 4, *Hill 6061* (TAES, TEX); Comal Co., New Braunfels, *Lindheimer 682* (BR, F, GH, NY, PENN, TEX, US, VT); DeWitt Co., 2 mi. SW of Yoakum, *Hill 7715* (SMU, srh, TAES, TEX, US, VT, WIS); Duval Co., San Diego, *Croft 215* (NY); Edwards Co., TAES Research Institute, substation 14, *Cory 38348* (TEX); Gillespie Co., *Jermy s.n.* (MO); Goliad Co., ca. 9 mi. SE of Goliad near the San Antonio River, *Hill 5889* (GH, pf, srh); Gonzales Co., *Whitehouse s.n.* (TEX); Harris Co., Houston, *Hill 4579* (srh, TEX); Hidalgo Co., Mission, *Clover 113* (MICH); Jackson Co., S of Vanderbilt, *Barkley & Tharp 13A142* (GH, MO, NY, PH, SMU, TEX); Jeff Davis Co., 12 mi. N of Alpine, *Hinckley 4890* (US); Jim Wells Co., Premont, *Johnston 541537* (TEX); Karnes Co., 1.25 mi. SW of Helena, *Johnson 802* (CAS, TAES, TEX); Kenedy Co., Saltillo Pasture, *Johnston 541662* (TEX); Kinney Co., Fort Clark, *Mearns 1402* (US); Kleberg Co., Kingsville, *Bogusch 11893* (US); La Salle Co., 6.5 mi. W of Fowlerton, *Cory 28520* (GH); Lavaca Co., Hwy. 77, 1.2 mi. N of FM 532, *Hill 7958* (CTES, pf, SMU, srh, TEX); Live Oak Co., Grant Ranch, *Tharp s.n.* (MO, SMU); Matagorda Co., 1.5 mi. W of Bay City, *Cory 51103* (DS, GH, MICH, NY, SMU, UC, US); Maverick Co., 9 mi E Eagle Pass, rte 277, *Correll & Johnston 19470* (FSU, TEX;) McMullen Co., 1.7 mi. N of Tilden, *Shinners 16966* (SMU); Medina Co., 23 mi. NE of Hondo, *Cory 34957* (TAES); Nueces Co., Robstown, *Wolcott & Barkley 16T402* (SMU, TEX); Pecos Co., *Buckley s.n.* (NY); Real Co., Frio River at Leakey, *Cory 44502* (TAES); Refugio Co., ca. 5 mi. S of Refugio, FM 2678, *Hill 5112* (MO, NY, SMU, srh, TAES); San Patricio Co., Welder Wildlife Refuge, *Board 1106a* (pf); Travis Co., Austin, *Bodin 127* (US); Uvalde Co., Uvalde, *Palmer 104* (K, NY, US); Val

Verde Co., Del Rio, *Correll 14966* (TEX, UC, US); Victoria Co., 7 mi. SW of Victoria, *Hill 6362* (SMU, TAES, TEX); Webb Co., 3 mi. NE of Laredo, *Earles & Villarreal 64* (SMU, TEX); Willacy Co., 3 mi. S of Raymondville, *Shinners 17114* (SMU); Zapata Co., *Board 1102* (pf); 2.8 mi. N of San Ygnacio, *Shinners 30860* (SMU).

MEXICO. BAJA CALIFORNIA: Dist. del Sur, San José de Comondú, *Carter et al. 2112* (DS, UC); CAMPECHE: Tuxpeña, *Lundell 1255* (DS, GH, MICH, MO, NY, UC, US); CHIAPAS: 22 km. N of Tuxtla Gutiérrez, *Breedlove 20019* (DS, pf); COAHUILA: 35 mi. NW of Múzquiz, *Fryxell 2681 (pf,* TEX); COLIMA: Manzanillo, *Palmer 1041* (GH, NY, US); DURANGO: Durango City, *Palmer 203* (GH, K, MO, NY, UC, US); GUANAJUATO: 14 mi. SE of León, *Waterfall & Wallis 13894* (SMU); GUERRERO: Atoyac, Galena, *Hinton 14558* (GH, NY, PH, TEX, US); HIDALGO: Dist. Jacala, Jacala to Pacula, *Moore 1808* (BH, GH); JALISCO: between Jamon and Guadalajara, *Gregg 850* (MO); MÉXICO: Mun. Tepozotlan, Paso de la Concepción, *Alonso s.n.* (ENCB); MICHOACAN: Punguato, near Morelia, *Arsène s.n.* (MO, US); MORELOS: Cuernavaca, *Pringle 9075* (CU, GH, MO, US, VT); NAYARIT: 15 km. SE of San Blas, *Feddema 978* (MICH, TEX); NUEVO LEÓN: 2 mi. N of Sabinas Hidalgo, *Barkley et al. 14524A* (GH, MO, PH, TAES); OAXACA: Oaxaca, *Ernst 2270* (US); PUEBLA: 8.5 mi. N of Matamoros, *Dunn & Dunn 18768* (pf); QUERÉTARO: Querétaro, *Arsène 10611* (MO, US); QUINTANA ROO: Cozumel Isl., *Steere 2965* (MICH); SAN LUIS POTOSI: Tamazunchale, *Edwards 447* (DS, GH, MO, NY, PENN, SMU, TEX, UC); SINALOA: Culiacán, *Brandegee s.n.* (US); SONORA: Sonora Alta, *Coulter 799* (GH, NY); TAMAULIPAS: 90 km. NW of Tampico, *Percival s.n.* (pf); VERACRUZ: 3 km. E of Tuzamapan, Coatepec, *Corral-Lorenzoni 13* (pf); Papantla, *Fryxell 720a* (pf); YUCATAN: Chichen Itzá, *Rose M521* (RSA); ZACATECAS: San Juan Capistrano, *Rose 2446* (US); **GUATEMALA.** GUATEMALA: Guatemala City, *Harmon 2021* (UMO); PETEN: La Libertad, *Aguilar 83* (G, MICH, NY); ZACAPA: Zacapa, *Kellerman 2931* (NY); **BELIZE.** Dist. Cayo, Grano de Oro, *Croat 23381* (MO); **EL SALVADOR.** San Salvador, *Calderón 154* (GH, MO, NY, US); **HONDURAS.** SWAN ISLAND: *Nelson 95* (GH); TEGUCIGALPA: El Zamorano, campus, *Molina 25891* (MO, NY); YORO: Quebrada Seca, *Standley 53929* (US); **NICARAGUA.** ESTELÍ: Mechapa, *Atwood 984* (VT); MADRIZ: 2 km. S. of Yalaguina, *Hamblett 797* (NY, SMU); MATAGALPA: Matagalpa, *Williams et al. 23821* (TEX); **COSTA RICA.** GUANACASTE: Hacienda Valle Brimont, *Brenes s.n.* (NY); LIMÓN: Port Limón, *Greenman & Greenman 5273* (MO); **PANAMA.** PANAMA: near Panama City, *Standley 27691* (C, US); CANAL ZONE: Ancón, *Piper 6015* (US); TABOGA ISLAND, *Standley 27837* (US).

BERMUDA. N of Hamilton, *Brown & Britton 248* (BKL, K, NY, PH, US); **BAHAMAS.** ELEUTHERA: Governor's Harbour, *Britton & Millspaugh 5461* (NY); NEW PROVIDENCE: Nassau, *Wight 196* (GH); **CUBA.** ISLA DE PIÑOS: Caleta Crocodrilos, *Britton et al. 15324* (NY, US); CAMAGUEY: La Gloria, *Shafer 172* (NY, US); HABANA: near Marianao, *León 629* (NY); LAS VILLAS: Río San Juan, *Britton et al. 5932* (NY); MATANZAS: Tomory Valley, N of Matanzas, *Rugel 35* in part (NY, pf); ORIENTE: Santiago, *Clemente 5329* (GH, NY); PINAR DEL RÍO: Guanajas, *Palmer & Riley 798* (NY); **HAITI.** TORTUE ISLAND: La Valleé, *Leonard & Leonard 11558* (MO, NY, US); NORD-OUEST: Bassin Bleu, *Leonard & Leonard 14900* (US); NORD: Plaisance, *Leonard 9236* (GH, UC, US); ARTIBONITE: Ennery, *Leonard 8948* (PH, US); OUEST: Port au Prince, *Rose 23992* (US); **DOMINICAN REPUBLIC.** AZUA: Azua, *Rose & Firch 3947* (NY); BARAHONA: Barahona, *Howard & Howard 8468* (GH, NY); MONTE CRISTI: Monción, *Valeur 751* (C, MICH, US); PLATA: Puerto Plata, *Raunkiaer 1184* (US); SANTIAGO:

Herradura, *Jiménez* 1331 (CAS, US); SANTO DOMINGO: Santo Domingo, *Ekman 11380* (B, US); **PUERTO RICO.** AGUADILLA: Rincón, *Sintenis 5532* (B, NY, US); GUAYAMA: Aibonito, *Sintenis 2954* (G, US); MAYAGÜEZ: Guanica, *Britton et al. 4882* (NY); PONCE: Caja de Muertos, *Britton et al. 4984* (NY); SAN JUAN: Bayamón, *Sintenis 1034* (G, MO, NY); CULEBRA ISLAND: *Britton et al. 240* (NY, US); VIEQUES ISLAND: Isabel Segunda, *Shafer 2508* (CAS, NY, US); **VIRGIN ISLANDS.** ST. CROIX: Bassin Yards, *Ricksecker 4* (GH, MO, NY, UC, US); ST. THOMAS: Villa Olga, *Croat 75* (MO, US); TORTOLA: *Fishlock 24* (CAS, NY, US); **JAMAICA.** MIDDLESEX: Kingsland, *Adams 13149* (MO); SURREY: Kingston, *Harris 6851* (F, US); **ST. MARTIN.** *Shiffers 2347* (GH); **ST. BERTHELEMY.** Morne, Grand Bous, *Questel 199* (NY); **ST. EUSTATIUS.** Orangestad, *Shiffers 3860* (GH); **ANTIGUA.** Gunthorpes, *Box 920* (MICH, MO, pf, US); **GUADELOUPE.** GUADELOUPE. Basse-Terre, *Duss 2333* (NY, US); LA DESIRADE: Grande Anse, *Proctor 21287* (GH); **MARTINIQUE.** St. Pierre, *Duss 859* (MO, NY); **ST. VINCENT.** Ft. Charlotte, *Morton 4827* (US); **BARBADOS.** Bathsheba, *Waby 102* (US); **GRENADA.** Richmond Hill, *Broadway s.n.* (GH); **TOBAGO.** Buccoo Bay, *Purseglove 6263* (K, US); **TRINADAD.** Pointe Gourde, *Britton & Broadway 2650* (GH, NY, US); **CURAÇÃO:** St. Thomas College, *Arnoldo 2126* (US).

GUYANA. Georgetown, *Irwin T-40* (TEX); **VENEZUELA.** ARAGUA: Maracay, *Cornelio 153* (US); DISTRITO FEDERAL: La Florida, near Caracas, *Alston 5205* (BM); LARA: Bariquisimeto, *Saer 592* (F); TACHIRA: La Guanja near Rubio, *Farenholtz 2023* (U); **COLOMBIA:** ANTIOQUIA: Medellín, *Archer 3* (US); BOLIVAR: Cartagena, *Heriberto 113* (US); BOYACÁ: Guateque, *Arbelaez 419* (US); CALDAS: La Jopa, Río Paez, Tolima, *Lehmann 7823* (GH, US): CUNDINAMARCA: Soacha, near Bogotá, *Apollinaire & Arthur 111* (US); MAGDALENA: Santa Marta, *Smith 730* (DAO, G, GH, MICH, MO, NCU, NY, PH, UC, US, VT, WIS); SANTANDER: Galán, *Rueda-P. 297* (US); VALLE DEL CAUCA: Plana del Valle, Zarzal, *Cuatrecasas 22117* (F); **ECUADOR.** GUAYAS: Playas, *Asplund 5101* (NY); GALÁPAGOS: Charles (Santa Maria) Island, *Andersson s.n.* (GH); Chatham (San Cristóbal) Island, western portion, *Schimpff 129* (BKL, CAS, G, MO, NY, U); **PERU.** HUÁNUCO: Huánuco, *Asplund 13483* (G, US); LIMA: Chosica, *Stafford 37* (K); **CHILE.** SANTIAGO: Santiago, *Gigoux s.n.* (GH); TARAPACÁ: Arica, *Jaffwell 1093* (GH); **BOLIVIA.** BENI: Reyes, *Rusby 1418* (MICH, NY, US); COCHABAMBA: Cochabamba, *Shepard 261* (CAS, GH, NY, US); LA PAZ: Coripata, Yungas, *Bang 2111* (G, GH, K, MICH, MO, NY, PH, US); SANTA CRUZ: El Palmarito, Cabezas, Cordillera, *Perecho 322* (GH); **BRAZIL.** AMAZONAS; upper Río Negro River, *Weiss & Schmidt s.n.* (NY); BAHIA: *Luschnath 170* (BR); CEARÁ: Sitio Clementes, Quixcara, *Leite 3* (CAS); GUANABARA: Río de Janeiro, *Dusén 87* (GH, NY, US); MINAS GERAIS: Juiz de Fora, *Holway & Holway 1409* (US); PARANÁ: Porecatu, *Hatschbach 23472* (MICH, NY, UC); PERNAMBUCO: Tapera, *Pickel s.n.* (B, BH, DS, GH, MO, PH, US); RIO GRANDE DO SUL: São Leopoldo, *Eugenio 113* (NY); SANTA CATARINA: Itajaí, *Conrad & Dietrich 2125* (MO): SÃO PAULO: Campinas, *Holway & Holway 1700* (GH, US); **ARGENTINA:** BUENOS AIRES: Alsina, *Krapovickas 3309* (NY); CHACO: Dpt. Resistencia, Laguna Blanca, *Hovimber 39* (GH); CORRIENTES: 26 km. SE of Libertador, *Krapovickas et al. 27427* (MO); FORMOSA: Guaycole, Formosa, *Jorgensen 3159* (MO, US); Dpt. Pilcomayo, Isla Yobay Guazú, *Morel 8095* (GH); MISIONES: Dpt. San Ignacio, Isla Pindoi-corpus, *Krapovickas 2361* (F, MO); SANTE FE: Dpt. San Cristóbal, Ceres, *Balegno 562* (MO); **PARAGUAY.** ASUNCIÓN: Pilcomayo River, *Morong 995* (GH, MO, NY, PH, US); CONCEPCIÓN: near Concepción, *Hassler 7417* (BM, G, NY, UC); río Apa, calcareous region,

Hassler 11217 (A, G, GH, K); SAN PEDRO: Alto Paraguay, *Woolston 250* (NY); **URUGUAY.** Cuaresin (Antigos), *Berro 1568* (C);

MADEIRA ISLANDS. MADEIRA: Funchal, *Bornmüller 375* (BR); **GHANA.** ASHANTI: Cadbury Hill, Kumasi, *Darko 594* (MO); EASTERN PROVINCE: New Jafo, *Levi 4094* (MO); **SOUTH AFRICA.** EAST CAPE: Port St. Johns District, *Mogg s.n.* (MO, NY); NATAL: Pietermaritzburg Distr., *Kapi 37* (MO); TRANSVAAL: Distr. Zootpansberg, 42 mi W of Louis Trichardt, *Schleben 7545* (B); **KENYA.** Nairobi, *Lambinon 75/262* (MO); **NIGERIA. Oyo,** Ibadon, *Kea & Stanfield 37064* (B); **FARQUHAR ATOLL.** *Stoddart & Poome 1378* (US); **MADAGASCAR.** Prov. Diego Suarez, D'Antoirane, *Viguier & Humbert 131* (B); **INDIA.** ANDHRA PRADESH: E. Godavari, *Wagh 1697* (MO); BENGAL: Bengal and Madras, *Thomson s.n.* (G, GH); DELHI: Delhi, *Dewan s.n.* (TEX); HIMACHAL PRADESH: Pathankot, *Stewart 1767* (BH, MO, NY, PH); KASHMIR: Muzaffarabad, Azadkashmir, *Qaiser & Abedin 9189* (US); MADRAS: Hosur Taluk, Salem, *Yeshoda 129* (B, GH, NY); MYSORE: Hassan, *Saldanha 13573* (US); ORISSA: Pottangi, *Mooney 3910* (GH, MO, NY); PUNJAB: Bhadwar, Kangra, *Koelz 4094* (GH, MICH, NY); RAJASTHAN: Dungarpur, *Verma 171* (MO); UTTAR PRADESH: Etawah, *Dudgeon & Kenoyer s.n.* (MO); **WEST PAKISTAN.** KARACHI: Ayub Park, *Quaiser 243* (NY); LAHORE: Gujranwala distr., Khongah Dagram, *Stewart 1432* (GH); SARGODHA. Bagh-a-Jinah, *Abedin 2377* (BH, MO); **SRI LANKA (CEYLON).** UVA; Matale District, road from Naula to Daubulla, *Howicke et al. 316* (F, MO, NY); **BURMA.** Mandalay, *White 59* (US); **VIETNAM.** Da Nang, *Clemens & Clemens 3957* (CAS, G, GH, MICH, MO, NY, pf, PH, US); **HONG KONG.** Kowloon, *Hu 10696* (US); **CHINA.** FUKIEN: Fu-chou, Chong Chen Sang, *Tang 6653* (WIS); KWANGTUNG: Honam Island, *Levine 820* (GH, MO, US); **TAIWAN.** Little Quemoy, *Chuang s.n.* (GH); **RYUKYU ISLANDS.** MIYAKO JIMA: SW of Tanani, *Fosberg 38173* (NY, US); OKINAWA: Naha *Walker et al. 5739* (US); **PHILIPPINES.** LUZON: Manila, *Merrill 451* (GH, MO, NY, US); MINDORO: Mt. Yagaw, *Conklin 18662* (GH); SULU ARCHIPELAGO: Cebu, *McGregor 1685* (NY, US); **INDONESIA.** JAVA: Garoet, *Millspaugh 3091* (F); LOMBOK: *de Voogd 2066* (NY); **CELEBES.** BITUNG (BILLITON) ISLAND: *Alston 16596* (GH); **MOLUCCAS.** BABON ISLAND: Letwurung, *Borssum-Walkes 3077* (GH); **BRITISH NORTH BORNEO.** Bumbun, *Wood 2298* (UC); **NEW GUINEA.** Mordee distr., Finschafen, *Clemens 4278* (GH); **AUSTRALIA.** NORTHERN TERRITORY: Mitchell Station, Darwin, *Nelson 1011* (AD); QUEENSLAND: Jericho, Mitchell distr., *Clemens s.n.* (GH, MICH); NEW SOUTH WALES: Casino, *Betche s.n.* (G); HERON ISLAND: Capricorn group, *Fosberg 55058* (US); LORD HOWE ISLAND: Transit Hill, *Greene s.n.* (GH); **BONIN ISLANDS.** HAHA-JIMA: *Wilson 8285* (GH, US); **MARIANAS.** AGRIHAN ISLAND: *Fosberg 31436* (US); ALAMAGAN ISLAND: *Falanruw 1938* (US); SAIPAN ISLAND: Fanuchuluyan Bay, *Fosberg 31340* (US); TINIAN ISLAND: *Fosberg 24900* (NY, US); ROTA: *Fosberg 31904* (NY, US); GUAM: *Fosberg 32640* (NY, US); **NEW CALEDONIA.** NOUMÉA: Nouméa, *Franc 808* (F, G, GH, NY, UC, US); **FIJI.** Voli voli, Nadronga, *Koroiveibau 10667* (GH, NY, US); **ILES DE HORN.** ALOFI: *Yuncker 10033* (US); **TONGA.** Pangai (Haapai), *Soakai 304* (GH); TONGATAPU ISLAND: Village of Fu'amotu, *Yuncker 15162* (US); **HAWAIIAN ISLANDS.** MIDWAY ISLAND: Sand Island, *Fosberg 35704* (US); KAUAI: Niumalu Bay, *Degener 8979* (NY); OAHU: Keena Military Reservoir, *Degener & Degener 31765* (A, NY); LANAI: Palawai, *Munro 183* (NY); HAWAII: Hoolehua, Molokai, *Degener 6066* (CAS, MO, NY, US); FANNING ISLAND: *Herms & Kirby s.n.* (DS, GH, UC); **COOK ISLANDS.** Rarotonga, Ruarua, *Philipson*

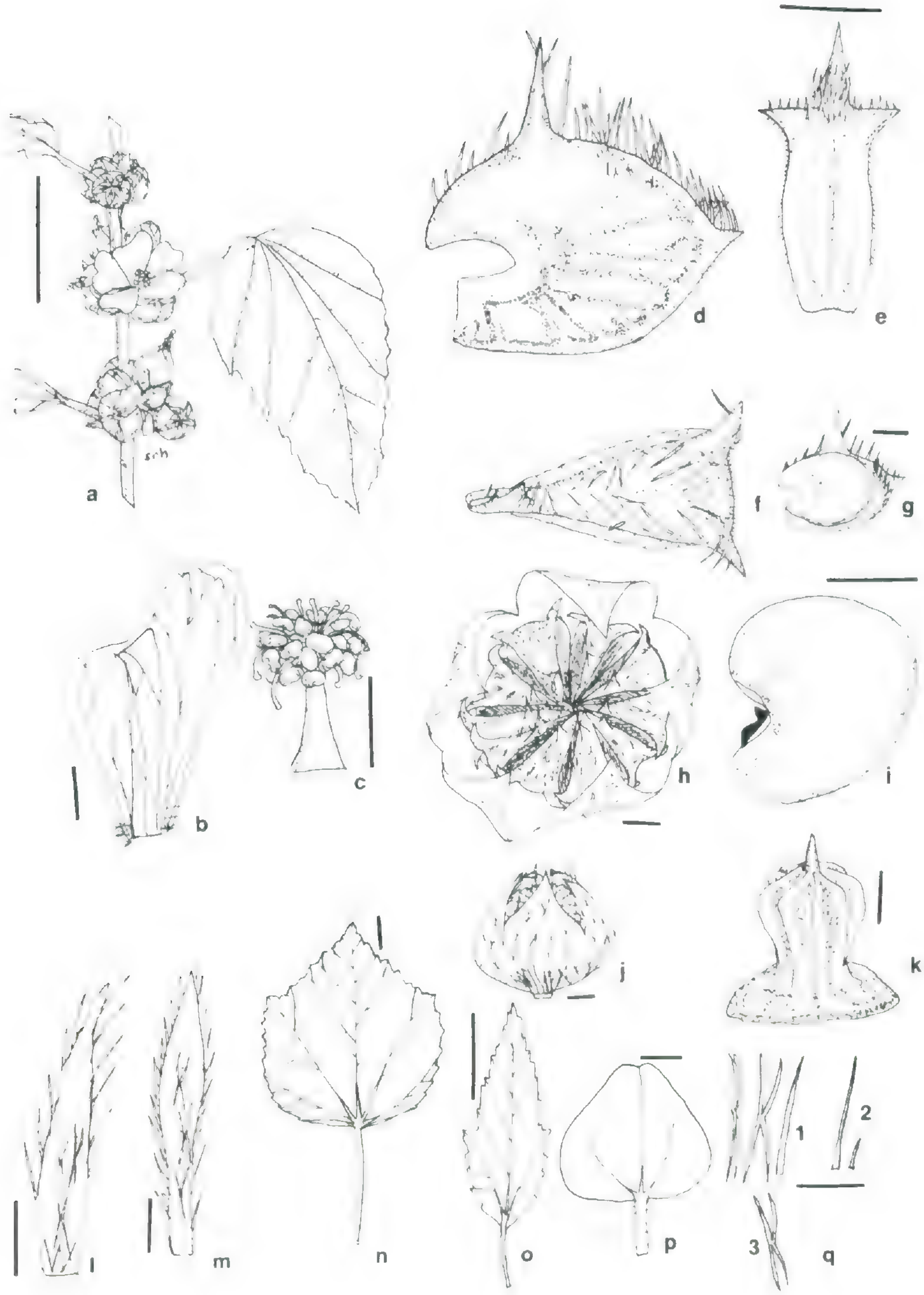
10343 (US): **SOCIETY ISLANDS.** RAIATEA: Uturoa, *Moore 193* (MO, RSA); **MARQUESAS.** HIVA'OA: Hanamenu Valley, *Decker 1294* (MO, RSA); NUKU HIVA: *Moore 161* (US); UAPU: *Moore 505* (US); UA HUKA: *Decker 1476* (US); WASHINGTON ISLAND: *Bergman 88* (UC); **TUAMOTU.** Raroia Atoll, *Doty & Newhouse 11710* (US); **PITCAIRN ISLAND.** *Chapin 989* (NY); **GAMBIER ISLANDS.** MANGARÉVA: *Agassiz et al. 121* (GH, US); **EASTER ISLAND.** *Agassiz 61* (GH).

13b. Malvastrum coromandelianum (Linnaeus) Garcke subsp. **capitato-spicatum** (O. Kuntze) S.R.Hill, Brittonia **32**(4): 476. 1980. Fig. 67

Malveopsis coromandeliana (Linnaeus) Morong var. *capitato-spicatum* O. Kuntze, Rev. Gen. **3**(2): 21. 1898. TYPE: Argentina. Córdoba: presumably *O. Kuntze,* not seen. See Hill (1980) for discussion. *Malvastrum tricuspidatum* (R. Brown in Aiton f.) A. Gray var. *β capitato-spicatum* (O. Kuntze) Stuckert, Anales Soc. Ci. Argent. **114**: 28. 1932.

Malvastrum coromandelianum (Linnaeus) Garcke var. *congestum* R. E. Fries, Ark. Bot. **6** (2): 6. 1906. TYPE: Argentina. Jujuy: Quinta, in fields, 2 June 1901. *R. E. Fries 69* (HOLOTYPE: S!). *Malvastrum tricuspidatum* (R. Brown in Aiton f.). A. Gray var. *congestum* (R. E. Fries) Stuckert, Anales Soc. Ci. Argent. **114**: 28. 1932.

Suffruticose erect perennial or annual herb (0.3) 0.6–1.5 mm tall; *main stem* (4) 6–7 (10) mm diam at base, branches up to 30–40 cm; stem *vesture* of longitudinally scattered narrowly bilateral closely appressed short-tuberculate (2–3) 4-rayed stellate hairs rarely mixed with simple hairs 1.0–2.0 mm long; *cotyledons* 13–15 mm long × 12–13 mm wide, wide-ovate, unlobed; *stipules* (4) 6–8 (10) mm long × 0.8–1.5 mm wide, subfalcate, lanceolate, acuminate; *petioles* 30–40 (55) mm long, to (8) 15–25 mm long in apical leaves; *blades* 1.4–2.0 (2.5) to 2.8–4.0 (4.7)× longer than the petioles in basal and apical stem leaves respectively, 60–90 (110) mm long × 40 60 (110) mm wide in lower stem leaves reduced to (25) 40–50 (75) mm long × (15) 20–30 (40) mm wide in upper leaves, average midstem blade (1.1) 1.4–1.8 × longer than wide, wide-ovate to ovate-lanceolate, unlobed or not infrequently shallowly 3-lobed 1/2 to 2/3 way from the broadly rounded subtruncate to wide-cuneate base, apex acute to acuminate, margin dentate to nearly serrate with 2–3 (4) teeth/cm, vesture of the adaxial surface of bilateral 4-rayed apically or marginally directed appressed stellate hairs (0.3) 0.5–1.0 mm long, abaxial surface similar; *flowers* not precocious, solitary in the axils of leaves and stipules but soon produced in congested axillary and terminal few to many-flowered glomerate or short-spicate racemes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throughout the upper half of the plant conspicuously separated by internodes 1–2 cm long, main branches usually with more than one open flower/day; bifid *floral bracts* lacking, flowers subtended by reduced leaves with stipules or by stipules alone; *pedicels* (1) 2–3 (15) mm long in young plants to 0.5–1.0 mm in inflorescences, not lengthening in fruit; *involucel* of 3 lanceolate to narrowly lanceolate slightly falcate acuminate bracteoles 4–6 mm long × 0.5–0.7 mm wide united 0.5–1.0 mm basally to calyx; *calyx* united 2/5 to 1/2 its length, 5–6 mm long to 8–12 mm long in fruit, broadly campanulate, lobes slightly spreading in flower and erect or incurved in fruit, deltate-cuspidate, 3–4 mm long × 2–2.5 mm wide to 4–5 mm long × 3–4 mm wide in fruit, abaxial surface moderately to sparsely pubescent with primarily 4-rayed stellate hairs 0.3–1.5 mm long on the veins and a ciliate margin of simple hairs 0.5–1.2 (2.0) mm long, adaxial surface puberulent with minute arachnoid simple or obscurely stellate hairs on the apical 1/2 to 2/3 and marginally to the sinus; *corolla* yellow to pale golden-yellow, 15–17 mm diam when spread, wide-campanulate at anthesis or nearly rotate, the petals asymmetrically bilobed, 7–9 mm long × 5–6 mm wide exceeding calyx by 3 mm, claws ciliate on the basal margins with a few simple tufted hairs 0.4–0.6 mm long; *androecium* with 16–26 stamens, filament tube 0.9 mm long; *gynoecium* with 11-13 carpels, style branched 2–2.5 mm above the columella, each stigma conspicuously expanded and hemispherical to subglobose and subequal to slightly recurved below the anther cluster; *schizocarps* 5.5–6.5 (9) mm diam including ornamentation; *mericarps* 11–13, 3.0 4.5 mm in height × 3.0–4.0 mm in length × 1.3–1.5 mm in width including ornamentation, with a single medial-apical cusp 1.0–2.0 mm long 1.0–1.2 mm distal to the proximal margin and two distal-apical cusps (0.3) 0.4–0.7(1.0) mm

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Figure 67. **Malvastrum coromandelianum subsp. capitato-spicatum. a.** Inflorescence habit, scale = 2 cm. **b.** Petal, scale = 2 mm. **c.** Stamens, styles and stigmas, scale = 2 mm. **d.-f.** Mericarp, lateral, distal and apical views, scale = 1 mm. **g.** Mericarp, internal view, scale = 1 mm. **h.** Fruit, apical view, scale = 2 mm. **i.** Seed, lateral view, scale = 1 mm. **j.** Calyx in fruit, lateral view, scale = 1 mm. **k.** Columella, scale = 0.5 mm. **l.** Stipule, scale = 1 mm. **m.** Bracteole, scale = 1 mm. **n.** Leaf, midstem of young vegetative plant, scale = 2 cm. **o.** Leaf, upper stems, second year plant, scale = 2 cm. **p.** Cotyledon, scale = 5 mm. **q.** Hair types, 1) stem, 2) mericarp, 3) leaf, scale = 0.5 mm. (a-b, d-i, l-p from plants grown from *Varela 52;* c, j-k from plants grown from *Morel 5794;* q from *Fries 69.*) Reprinted from Hill, 1980.

long conspicuously divergent from one another, lateral faces conspicuously ribbed especially on the margins, vesture of the apical surface and cusps of rigid simple hairs 0.6–1.0 mm long infrequently mixed with a few minute 2–5-rayed stellate hairs 0.05 mm diam, lateral faces glabrous or a few minute hairs near apex, distal surface with a raised medial line and minutely pubescent with medial and marginal simple or stellate hairs, mericarp indehiscent or loosely sealed along the proximal-apical margin, endoglossum lacking, readily shed from the receptacle and calyx at maturity; *seeds* 1.7–2.0 mm in height × 1.8 2.1 mm in length ×0.7–0.9 mm in width; *chromosome number:* $n = 12$, $2n = 24$; *pollen* 72–94.7 (80.7) μm diam, echinae 4–7.7 μm, apertures ca. 15–20.

Distribution. (Fig. 66) Occurring in the foothills and montane regions from Prov. Córdoba and San Juan, Argentina in the south to Salta and Formosa, Argentina in the north and in isolated stations to Cochabamba, Bolivia, and the Galápagos Islands from near sea level (in the Galápagos) to 400–2600 m.

Phenology and reproductive biology. Flowering March to May (local autumn) or infrequently as early as December; specimens collected in June and July bore old fruits only. Plants grown from seeds as much as 34 years old (*Fosberg 44742, Luna 1170, Morel 5794,* and *Varela 52*) germinated 4 6 days after planting and produced their first flowers after 40–60 days flowering continuously after that time until cold conditions caused them to become dormant. The progeny of *Fosberg 44742* grew to over 1 m before producing its first flowers (after 90 days growth) in September. In the other plants flowers were produced when at a height of 30 40 cm. The flowering period locally was 2 2:30 pm CST to 4 4:15 CST and the flowers closed before those of subsp. *coromandelianum* opened. The pollen was generally released directly onto the stigmas or the stigmas were dusted with pollen as the flowers wilted. Fruits matured in 17–21 days after pollination.

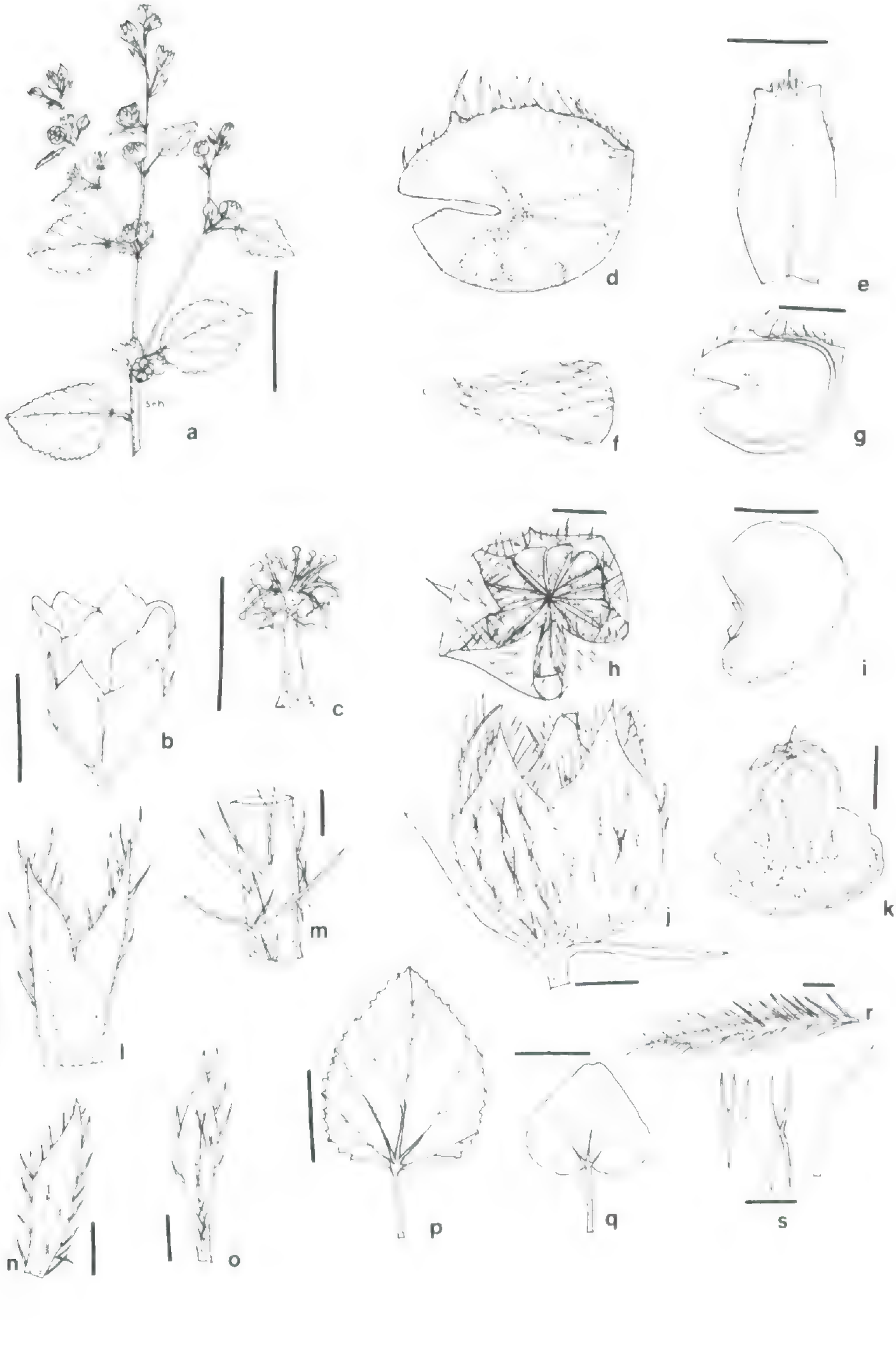
Discussion. This is a biological rather than a morphological subspecies since such characters as mericarp morphology and vesture are nearly indistinguishable from subsp. *coromandelianum.* From an early age plants produce glomerate axillary inflorescences and have large leaves that are the size (and sometimes the shape) of those of *Malvastrum americanum;* the flowers open (locally) early in the

afternoon, are almost exclusively autogamous, and close before those of *M. coromandelianum* subsp. *coromandelianum* open. The subspecies are separated by this phenological isolating mechanism. *Malvastrum coromandelianum* subsp. *capitato-spicatum* is best distinguished from subsp. *coromandelianum* by its dense, glomerate axillary inflorescences, much larger leaves (at least in youth), its adaxial leaf vesture of 4-rayed hairs only, its larger size, its very prominently cuspidate fruits (the cusps never reduced) and its occurrence primarily in the low sierra of north-central Argentina.

REPRESENTATIVE SPECIMENS: **ECUADOR.** GALÁPAGOS ISLANDS: Indefatigable Island (Santa Cruz), *Fosberg 44742* (MO); James Island (San Salvador), *Howell 9686* (CAS, GH); Chatham Island, *Howell 8518* (CAS); Charles Island, *Howell 9310* (CAS, K); **BOLIVIA.** COCHABAMBA: valle del Cercado de Cochabamba, *Steinbach 185* (SMU); **ARGENTINA.** CATAMARCA: Dpt. La Paz, Taco Pampa, *Brizuela 643* (MO); Dpt. Ancasti, Los Barriales, *Brizuela s.n.* (C, NY, RSA); Dpt. Andalgalá, edge of Río del Quebrado del Cura, 40 km W of Andalgalá, *Cantino 794* (GH); CÓRDOBA: Dpt. Córdoba, Gutemberg, *Bartlett 19878* (GH, MICH, UC, US); Córdoba, *Galander s.n.* (G, MO, NY, US); Dpt. Capital, Los Cuarteles, *Terribile 667* (SMU); FORMOSA: Dpt. Pilcomayo, Ruta 86, 2 km N of km 45, *Morel 5794* (MO, US); JUJUY: Dpt. Capital, Yala, *Krapovickas & Schinini 30718* (G); MENDOZA: Luján, *Leal 10152* (C); SALTA: Dpt. Viña, Coronel Moldes, *Hunziker 1135* (US); Dpt. Anta, Quebrachal, *Luna 117* (GH, MO); SAN JUAN: Dpt. Santa Lucia, *Cuezzo 2233* (SMU); SANTIAGO DEL ESTERO: Dpt. Surnampa, *Balegno 109* (NY); Dpt. Capital, *Lillo 41* (A, GH, UC); Dpt. Robles, Colonia Jaimes, *Luna 1170* (MO); SANTE FE: Las Rosas, *Beetle 914* (CAS); TUCUMÁN: Dpt. Capital, Lujau, *Venturi 83* (US).

13c. **Malvastrum coromandelianum** (Linnaeus) Garcke subsp. **fryxellii** S. R. Hill, Brittonia **32**(4): 480. 1980. TYPE: Brazil. Minas Gerais: 1 km. E of Río Pandeiros, road to Januária, elev. 520 meters, April 18, 1973. *W. Anderson, P. A. Fryxell, S. R. Hill, R. Reis dos Santos, & R. Souza 9096,* (HOLOTYPE: UB!; ISOTYPES: C!, K!, MO!, NY!, pf!, US!). Fig. 68, 69.

Herbaceous to suffruticose sparsely branched annual or perennial herb 0.4–1.0 m tall; *main stem* 3–9 mm diam at base, branches 30–60 cm long; stem *vesture* of perpendicular swollen-based simple hairs 1.0–2.0 mm long mixed with closely longitudinally appressed scattered bilateral 4-rayed stellate hairs 1.0–2.0 mm long tardily shed in age; *cotyledons* 8 mm long × 9 mm wide, wide-ovate, briefly emarginate at the apex and subcordate at the base; *stipules* 6–9 mm long × 0.8–1.2 mm wide, subfalcate to falcate, lanceolate to narrowly lanceolate, acuminate; *petioles* 10–26 mm long; *blades* 2.0–3.5×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longer than the petioles, (30) 35–50 (60) mm long × (12) 25–40 (55) mm wide progressively reduced towards branch apices, average midstem blade 1.3–1.5 × longer than wide, ovate, unlobed, base sub-truncate broadly rounded to wide-cuneate, apex acute, margin denticulate with 5–7 teeth/cm, vesture of the adaxial surface consisting of apically directed ascending simple hairs imparting a velvety or felty texture to the fresh leaf, abaxial surface with scattered primarily simple hairs like those on the stem mixed with a few 3–4-rayed bilateral stellate hairs 0.6–1.0 mm long; *flowers* solitary in the axils of leaves and stipules, at maturity on reduced glomerate axillary racemes or congested at the stem apex or on racemose branches and subtended by bifid *floral bracts* 5–6 mm long × 2 mm wide; *pedicels* 1.5–2.0 mm to 4–5 (7) mm in fruit; *involucel* of 3 narrowly lanceolate acuminate bracteoles 4–5 mm long × 0.5 mm wide, nearly free or adnate to calyx in the basal 0.5 mm; *calyx* united 1/3 to 1/2 its length, 5 mm long to 7–8 mm in fruit, campanulate in flower and fruit, the lobes slightly spreading in flower to nearly erect or slightly incurved in fruit, deltate-cuspidate, 2–2.5 mm long × 1.5–2.0 m wide to 5–6 mm long × 4–5 mm wide in fruit, abaxial surface sparsely pubescent with appressed 3–4-rayed bilateral hairs 0.5–1.0 mm long, veins and simple marginal hairs 0.4–0.8 mm long, adaxial surface minutely puberulent on the apical half and marginally to the sinus; *corolla* pale yellow-orange, 10–12 mm diam when spread, somewhat campanulate with slightly spreading lobes, petals asymmetrically bilobed, 6–7 mm long × 3 mm wide exceeding the calyx by 2 mm, claws pubescent at the basal margin with tufted simple hairs 0.1–0.5 mm long; *androecium* with 22–31 stamens, filament tube 1.5–2.0 mm long, glabrous, free portion of filaments 1.0 mm long; *gynoecium* with 10–11 carpels, the style branched 2.0 mm above the colu-

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Figure 68. **Malvastrum coromandelianum subsp. fryxellii.** **a.** Habit, scale = 5 cm. **b.** Flower, scale = 5 mm. **c.** Stamens, styles and stigmas, scale = 2 mm. **d.-f.** Mericarp, lateral, distal and apical views, scale = 1 mm. **g.** Mericarp, internal surface, scale = 1 mm. **h.** Fruit, apical view, scale = 2 mm. **i.** Seed, scale = 1 mm. **j.** Calyx in fruit, scale = 2 mm. **k.** Columella and carpocrater, scale = 0.5 mm. **l.** Floral bract, scale = 2 mm. **m.** Stem vesture, scale = 1 mm. **n.** Stipule, scale = 2 mm. **o.** Bracteole, scale = 2 mm. **p.** Midstem leaf, scale = 2 cm. **q.** Cotyledon, scale = 0.5 mm. **r.** Leaf in profile, vesture orientation, scale = 1 mm. **s.** Hair types of leaves, scale = 0.5 mm. (a from *Heringe 11483;* b-c, h, j-k, m, q and r from progeny of *Anderson, et al. 9096;* d-g, i, l, n-p, and s from *Anderson, et al. 9096.)* Reprinted from Hill, 1980.

Figure 69. **Malvastrum coromandelianum subsp. fryxellii** (isotype, US).

mella, each stigma conspicuously expanded and hemispherical to subglobose exserted 1.0 mm but recurved at flower wilt; *schizocarps* 5.0 mm diam including ornamentation; *mericarps* 10–11, 1.5–2.0 mm in height × 2.0 mm in length × 0.8–1.0 mm in width, with a small medial-apical cusp 0.2–0.4 mm long 0.8 mm distal to the proximal margin and 2 distal-apical cusps 0.1–0.2 mm long, lateral surfaces somewhat ribbed, distal-basal surface with an obscure raised medial line, vesture of the apical surface of rigid simple hairs 0.4–0.8 mm long, lateral and distal surfaces with a few apical minute simple hairs, mericarp indehiscent but loosely sealed or slightly dehiscent along the proximal-apical margin, endoglossum absent, readily or tardily shed depending on the orientation of the calyx lobes; *seeds* 1.4 mm in height × 1.3 mm in length × 0.7–0.8 mm in width; *chromosome number:* $2n = 24$; *pollen* 77–93 (84.3) μm diam, echinae 6–7 μm, apertures ca. 15–20.

Distribution. (Fig. 66) Known only from the Planalto region of south-central Brazil in the states of Goiás and Minas Gerais, with one specimen tentatively assigned here from Aragua, Venezuela (perhaps introduced), at elevations of 450–550 m.

Phenology and reproductive biology. Flowering March to June. Specimens grown from seed (*Anderson et al. 9096*) germinated in 4 days and produced their first flowers after 4 months of slow growth (120 days, in late October). The flowers opened at 3:30–3:45 pm CST and closed at 5:15–5:30 pm CST, after those of subsp. *capitato-spicatum*. A reliance on self-pollination is suggested by the approximate stigmas and anthers, but cross-pollination is also likely. Emasculated flowers did not set fruit.

Discussion. Malvastrum coromandelianum subsp. *fryxellii* is most closely allied to subsp. *capitato-spicatum* as seen in its somewhat glomerate inflorescences, but has several derived characters. These include the predominance of simple hairs, the presence of bifid floral bracts in age, and the small mericarps with reduced cusps. It probably represents a fairly ancient introduction to the Brazilian Planalto from the southern Pampean massif region. The reduction in cusp size probably occurred in its isolation and has prevented it from further extensive dispersal except in disturbed soils.

SPECIMENS EXAMINED. **VENEZUELA.** ARAGUA: University Central de Venezuela, Maracay, *Croat 21342* (MO); **BRAZIL.** GOIÁS: Gob. Goiás, Goiás, *Burchell 6925* (BR, K); Gob. Formosa, Río Tiquiri, *Heringe 11483* (NY, srh, UB); MINAS GERAIS: 1 km E of Río Pandeiros, road to Januária, *Anderson et al. 9096* (C, F, K, MO, NY, pf, US); Paraopeba, *Heringer 9360* (UB) and *9457* (UB); Lagoa Preta, *Heringer 6596* (UB).

Section 7. *Corchorifolium*

Malvastrum sectio **Corchorifolium** S. R. Hill, *sect. nov.*

Carpella matura 9–16, dehiscentia margine proximali-apicale solum, superficie apicale pilis stellatis minuto et simplicibus, muris lateralis percarpium crassis, ornata 2 mucronibus distali-apicalibus vel cuspidibus parvis 0.02 0.4 mm longis et mucrone unico mediali-apicale 0.02 0.4 mm longo, marginibus pericarpium angulatis, endoglosso minuto praesente; stamina 16 39, columnis staminalibus pubescentibus sparsim; flores solitariae axillares primo, demum in spicis parvis terminalibus; bracteolis involucellis adnatis basi calyce; bracteae florales bifidae praesentes; pili caulini stipitates nunquam; pollinis grana 15–25 aperturis; sectio origine hybrido probabiliter. TYPUS: *Malvastrum corchorifolium* (Desrousseaux in Lamarck) Britton ex Small.

The solitary axillary and later spicate flowers, indehiscent or weakly dehiscent thick-walled trimucronate mericarps, minute endoglossum, presence of bifid floral bracts, pubescent filament tube, and 15 25 aperturate pollen characterize the section *Corchorifolium*, a section of probable hybrid origin.

14. **Malvastrum corchorifolium** (Desrousseaux in Lamarck) Britton ex Small, Flora Miami: 119. 1913. Fig. 70, 71.

Malva scoparia Jacquin, Collect. **1**: 59. 1787; Icon. Pl. Rar. **1**: 14, t. 139. 1787, non L'Heritier, 1786. TYPE: in the absence of type material, t. 139 is chosen as lectotype. The plant was apparently raised from seed collected by Jacquin in Hispaniola ("insula Domingo"). The figure shows a young plant of the species with typical 4-rayed hairs and reduced or absent cusps. *Malva corchorifolia* Desrousseaux in Lamarck, Encycl. **3**: 755 (743 errore). 1792. Based upon *Malva scoparia* Jacquin, non L'Heritier.

Malva betulina Desrousseaux in Lamarck, Encycl. **3**: 754. 1792. TYPE: plants raised at Hortus Parisiensis in part from seed sent by Martín, Santo Domingo. The holotype has a large branch of this species (HOLOTYPE: P-LA), presence of holotype confirmed by Krapovickas (pers. comm.).

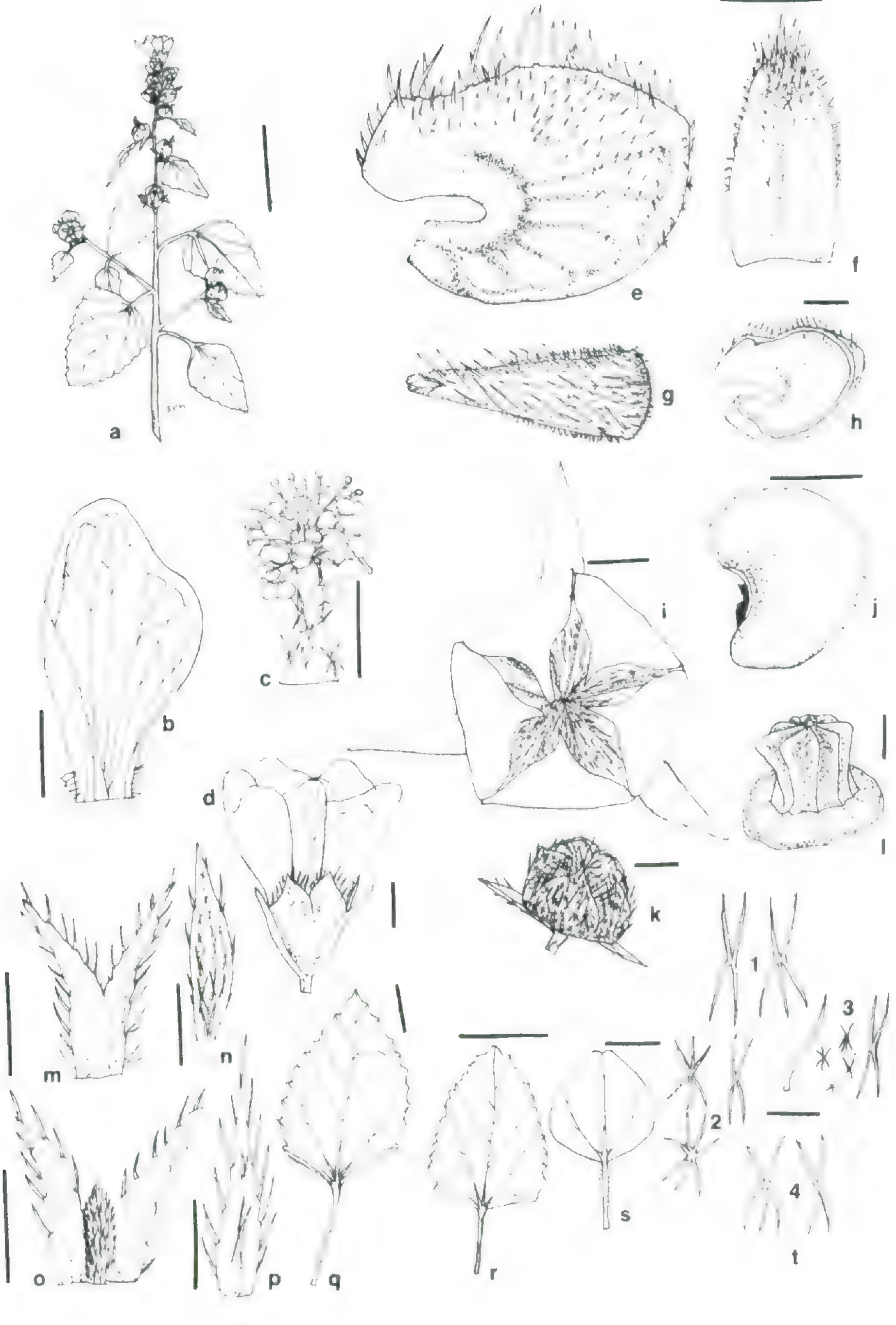
Malva americana sensu Willdenow, Enum. Plant.: 729. 1809, pro parte, non Linnaeus, 1753. This name, for the most part misapplied to *Malvastrum coromandelianum*, seems also to have included the present concept of *M.*

corchorifolium. A specimen in the Willdenow Herbarium (B-W) no. *12751*, sheet 3, from Santo Domingo, is probably *M. corchorifolium*.

Malva ulmifolia Balbis ex De Candolle, Prodromus **1**: 430. 1824, pro syn., nomen nudum. This name was listed as a synonym of *Malva americana* by De Candolle, who cited a Balbis specimen (TO - photo srh!) that appears to be *M. corchorifolium*.

Malvastrum rugelii S. Watson, Proc. Amer. Acad. Arts **17**: 367. 1882. TYPE: UNITED STATES. Florida: Manatee County, mouth of the Manatee River, calcareous soil, 1845. *F. Rugel 90* (HOLOTYPE: GH!; ISOTYPES: BM!, CU!, G!, pf!, UC!, US!).

Annual or perennial sparsely branched herb to 0.6–1.5 (1.8) m tall often suffruticose in age; *stem* 4–7 mm diam at base; *branches* up to 50–75 cm long; stem *vesture* principally of swollen-based longitudinally scattered appressed 4-rayed hairs 0.8–1.5 mm long or similar 3- or 5-rayed hairs; *cotyledons* 9–10 mm long × 10 11 mm wide, ovate to wide-ovate, petioles ca. 9 mm long; *stipules* (2) 3–5 (7) mm long × 0.8–1.2 mm wide, lanceolate to narrowly lanceolate, slightly falcate, narrowly acuminate; *petioles* (5) 15 35 (70) mm long; *blades* 1.8–2.2× longer than the petiole, (16) 30–50 (86) mm long × (8) 25–40 (75) mm wide, average midstem 1.5–1.6× longer than wide, ovate, unlobed, base broadly-cuneate to somewhat rounded, apex acute to rounded, margin dentate with 2.5–4.5 teeth/cm, vesture of the adaxial surface of sparse 4 5-rayed stellate hairs 0.3 1.0 mm diam and a few minute marginal simple hairs, vesture of the abaxial surface similar but with more 5 (6)-rayed hairs (6-rayed being more frequent in Central American populations); *flowers* solitary in axils of leaves and stipules later spicate on branch apices, in the axils of bifid floral bracts intermediate structures or stipules with reduced leaves, occasionally in reduced 2-6-flowered spikes in upper leaf axils; *floral bracts* divided 1/2 to 2/3 their length, 3 6 mm long×1.0 mm wide; *pedicels* (0.5) 1.0 (2.0) mm long scarcely increasing in fruit; *involucel* of 3 lanceolate acuminate slightly falcate bracteoles 4 6 (8) mm long × 0.8-1.0 mm wide united to calyx in basal 0.5–1.0 mm; *calyx* united 1/4 to 1/3 its length, 5–6 mm in height to 7–11 mm in fruit, broadly campanulate, lobes erect in flower and incurved in fruit, deltate-cuspidate, (3) 5 6 (7) mm long × (2) 3-4 mm wide, moderately pubescent on the abaxial surface primarily with rigid simple and 2-4-rayed hairs 0.5–1.2 mm long directed apically mixed with distinctly smaller scattered 4-6-rayed stellate hairs 0.05–0.2 mm diam (the hair types varying in proportion in different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populations but always of two distinct sizes), adaxial surface with a few minute arachnoid simple hairs near the margin and in the apical 1/4; *corolla* yellow to pale yellow-orange, broadly campanulate to nearly planar, petals asymmetrically bilobed, (5) 6–7 (8) mm long × 3–4 mm wide exceeding calyx by 2.0 mm, claws sparsely pubescent at the margins with simple hairs 0.2–0.3 mm long; *androecium* with (16) 23–33 (39) stamens, tending towards 25 and 30, filament tube 1.8–2.5 mm long, sparsely pubescent with appressed 2–4-rayed hairs 0.5 mm long, free portion of filaments 0.9–1.0 (1.5) mm long; *gynoecium* of (9) 11–13 (16) carpels, style branched 2 mm above the columella, each stigma subglobose to hemispherical and expanded raised above the anthers by 0.5 mm, occasionally recurved at anthesis and all recurved upon wilting; *schizocarps* (4.0) 5–6.5 (7.0) mm diam; *mericarps* (9) 11–13 (16), 2.0–2.5 mm in height × (2.2) 2.5–3 (3.5) mm in length × 1.0–1.2 mm in width, with 3 minute cusps (0.02) 0.1–0.2 (0.4) mm long, one on the proximal-apical surface but remote from the margin and two on the distal-apical surface, lateral faces moderately to strongly ribbed, moderately to densely pubescent on the apical distal and marginal third with minute simple or 2-rayed erect hairs, apical surface moderately pubescent with rigid erect simple hairs 0.5–1.0 mm long and sparse minute simple or 2–3-rayed stellate hairs, mericarp indehiscent except in the proximal-apical margin which is usually unsealed at maturity and occasionally somewhat tardily dehiscent in the proximal-basal region along the medial line, endoglossum 0.1–0.2 mm long, mericarps readily separating from the receptacle at maturity but often retained

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Figure 70. **Malvastrum corchorifolium.** **a.** Habit, scale = 5 mm. **b.** Petal, scale = 2 mm. **c.** Stamens, styles, and stigmas, scale = 2 mm. **d.** Flower, scale = 2 mm. **e.-g.** Mericarp, lateral, distal, and apical views, scale = 1 mm. **h.** Mericarp, internal view, scale = 1 mm. **i.** Fruit, apical view, vesture of calyx excluded, scale = 2 mm. **j.** Seed, scale = 1 mm. **k.** Fruit, vesture included, scale = 2 mm. **l.** Columella and carpocrater, scale = 0.5 mm. **m.** Floral bract, adaxial surface, scale = 2 mm. **n.** Bracteole, scale = 2 mm. **o.** Transitional bract, adaxial surface, scale = 2 mm. **p.** Stipule, abaxial surface, scale = 2 mm. **q.** Leaf, young vegetative plant, scale = 2 cm. **r.** Leaf of mature plant, scale = 2 cm. **s.** Cotyledon, scale = 5 mm. **t.** Vesture: 1) stem, 2) leaf, abaxial surface, 3) calyx, 4) leaf, adaxial surface, scale = 0.5 mm. (a, p from progeny of *Molina 27248;* b-d, i-k, from progeny of *Lakela & Pardue 31750;* e-g, l, n, r from *Correll 43867;* h from *Molina 11631;* m, t from *Molina 23070;* o from *Correll & Evans 44026;* q from *Correll 46320;* s from progeny of *Contreras 5588*).

Figure 71. **Malvastrum corchorifolium** (lectotype, Jacquin, Icon. Pl. Rar. 1: *t. 139. 1787*).

for a period by the incurved sepals; *seeds* 1.5–1.7 mm in height × 1.6–1.8 mm in length × 0.8–1.0 mm wide; *chromosome number: n* = 24, $2n = 48$; *pollen* 74.5–103 (89) μm diam, echinae 5–7 μm, apertures ca. 15–25.

Distribution. (Fig. 72) Found in generally coastal calcareous soil in the Caribbean area from Florida and the Bahamas in the north, east to the Lesser Antilles, west to Tabasco, Mexico and south in interior regions to Nicaragua, with a few introduced populations in the Cape Verde Islands and Ghana, at elevations from sea level to 1000 m.

Phenology and reproductive biology. Flowering and fruiting primarily from late October to late February in the Caribbean, but also flowering occasionally after rain throughout the year. Specimens from Chiapas were in flower August–September. In the greenhouse locally, progeny from Central American populations flowered three months (90–100 days) after germination, becoming dormant during the summer, and flowered again in the autumn. Progeny from Florida and the Caribbean that germinated at the same time in the spring did not flower until late autumn (October) continuing through the winter as in wild populations. The seeds (some as old as 46 years, i.e. *Steere 1010*) germinated in 5–14 days. The flowers opened in the late afternoon ca. 4 pm CST and closed at or before sunset at 6–6:15 pm CST. The time shifted an hour more or less according to seasonal daylength, but the duration was constant. The flowers always self-pollinated due to the close proximity of the stigmas and the anthers. Fruits mature in 24–36 days from pollination.

Discussion. About 30% of the specimens of *Malvastrum corchorifolium* examined had been misdetermined under the names *M. americanum* or *M. coromandelianum* depending on the maturity of the inflorescence. Once the chromosome number was confirmed as $2n = 48$ there was little doubt that this was a distinct species. An analysis of morphological characters demonstrated that the species possessed a mixture, in varying proportions, of characters exhibited by both *M. americanum* and *M. coromandelianum* (see discussion under phylogeny). The range of *M. corchorifolium* suggested that it was likely of Central American origin, and had expanded into the Caribbean, where it became particularly frequent on coastal lime-

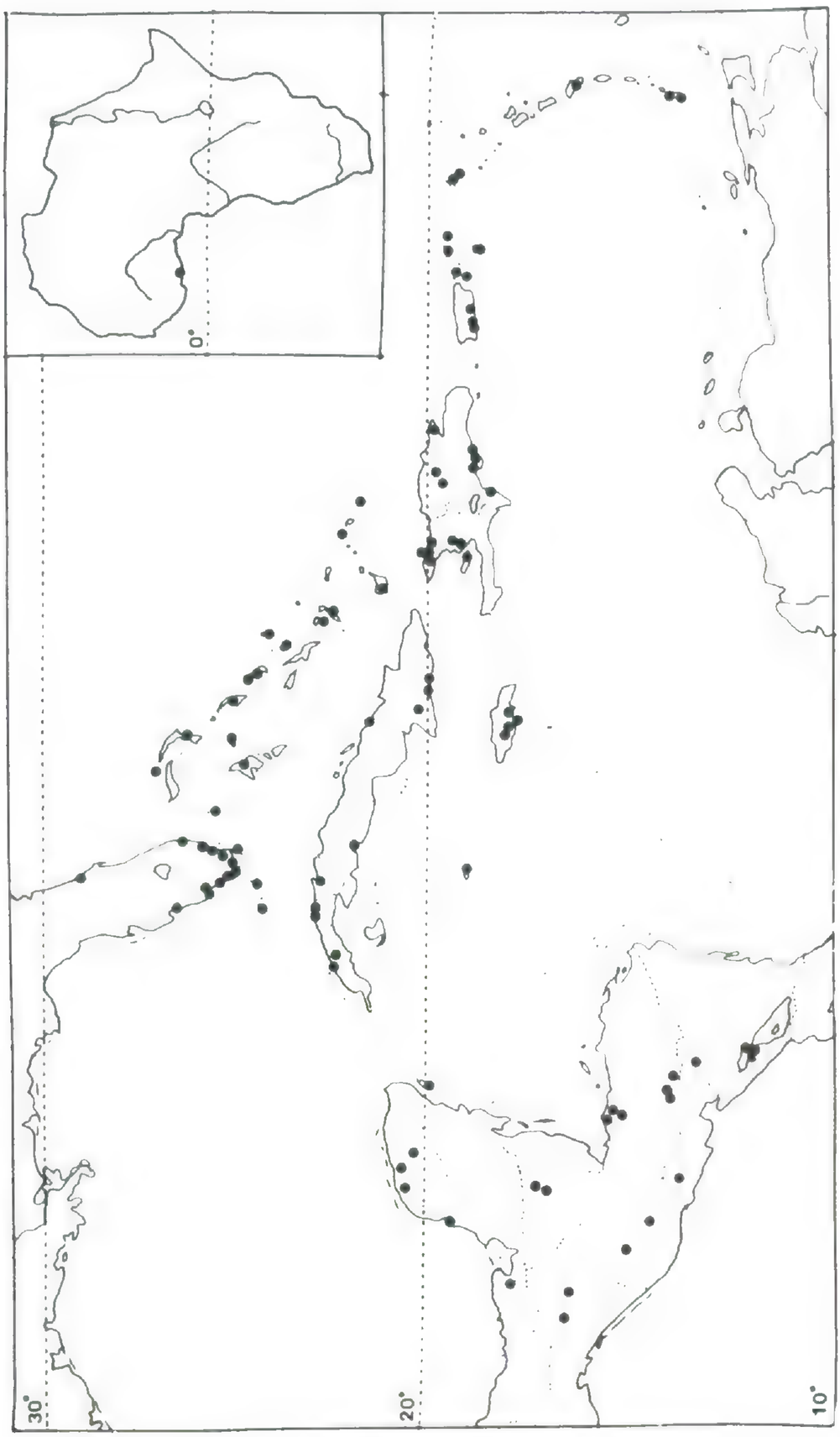

Figure 72. Distribution of Malvastrum corchorifolium.

stones. Formerly overlooked populations of the species from Nicaragua north through Mexico now support this hypothesis. I have proposed that *M. corchorifolium* is an allopolyploid derivative of *M. americanum* and *M. coromandelianum* and that it probably appeared in Central America after the appearance of the land bridge that increased the chance of hybridization between the two parental species.

Malvastrum corchorifolium is readily distinguished from *M. americanum* by its frequent bilateral 4-rayed hairs on all parts, by its sparse vesture on the calyx and leaves, by the unlobed leaves, and by the more densely pubescent mericarps (particularly on lateral surfaces) that often have three small mucros. It can be readily distinguished from *M. cormandelianum* where the ranges overlap by the lack of simple hairs on the adaxial leaf surface, by the dimorphic hairs of the calyx, by the reduced cusps, and by the spicate inflorescence that at maturity often has bifid bracts. *Malvastrum corchorifolium* is the most frequent *Malvastrum* in calcareous parts of the Caribbean. The disjunct population in Ghana, present since at least 1927 (Newton & Kisseadoo, 1978) was possibly introduced from the Caribbean during slave-trade along that particular region in Africa.

REPRESENTATIVE SPECIMENS: **UNITED STATES.** ALABAMA: Mobile Co., ballast at Mob. & O. Wharf, Mobile, adventive from Jamaica, *Mohr 35* (US); FLORIDA: Volusia Co., Turtle Mound Monument, south New Smyrna Beach, *Lakela & Pardue 31750* (DS, MO); Brevard Co., New Found Harbor, Cocoa, Cocoa Beach Rd, *Rhoads s.n.* (FLAS); Hillsborough Co., waste ground, *Fredholm 6407* (GH); Manatee Co., mouth of the Manatee River, Palmetto, *Nash 2462* (DAO, G, GH, MICH, MO, NCU, NY, PH, US); Lee Co., western Sanibel Island, *Brumbach 6081* (FLAS, US); Palm Beach Co., Palm Beach, *Hitchcock 202* (F); Broward Co., N of Hollywood Beach, Hollywood, *Churchill s.n.* (SMU); Collier Co., Marco Island, north end, *Lakela 27771* (FLAS, FSU, RSA, SMU); Dade Co., Miami, *Garber 80* (BUF, F, GH, MO, NY, PH, US, VT); southwest Miami, *Hill 3491* (pf, srh); Monroe Co., Big Pine Key, Watson Hammock, *Killip & Dickson 41601* (BH, CAS, F, GA, MICH, NY); Big Pine Key, *Lakela 27892* (GH).

BAHAMAS. ABACO: Cherokee Settlement, *Brace 2072* (F, NY); ACKLIN'S ISLAND: Duncan Hill, *Brace 4483* (F, NY); ANDROS: Nicholls Town, *Correll & Evans 44026* (FTG, NY); BIMINI: Cat Cay, north end, *Correll & Correll 45577* (F, FTG, NY, SMU); CAT ISLAND: The Bight and vicinity; *Britton & Millspaugh 5850* (F, NY); ELEUTHERA: Rock Sound, *Britton & Millspaugh 5567* (F, NY); FORTUNE ISLAND: *Hitchcock s.n.* (MO); INAGUA: Matthew Town, *Gillis & Proctor 12176* (A); LONG CAY: south side, *Brace 4114* (F, NY); NEW PROVIDENCE: Nassau, *Curtiss 47* (F, G, GH, MO, VT); RUM CAY: between Cistern and Port Nelson, *Correll & Wasshausen 46752* (F, FTG); SAN SALVADOR ISLAND: 1 mi. S of Finger Lake station, *Correll 43867* (F, FTG, NY); GRAND TURK: the ponds, *Millspaugh & Millspaugh 8999* (G, GH, NY); CAICOS ISLANDS: North Cai-

cos, W side of Whitby, *Correll 43267* (FTG, NY); ANGUILLA ISLES: Salt Key Bank, *Wilson 8065* (F, NY); **CUBA;** CAMAGUEY: Cayo Sabínal, Jatovieja, *Shafer 1054* (NY, US); HABANA: near Mayay, *Baker & Wilson 337* (GH, POM, US); LAS VILLAS: Cienequita, dist. Cienfuegos, *Combs 90* (GH, MICH, MO, NY, US); MATANZAS: from Tomory Valley to Matanzas, *Rugel 37* (MO, NY in part, pf); ORIENTE: Rente, Santiago Bay, *Clemente 2734* (GH); PINAR DEL RÍO: Buenaventura, *Wilson 9397* (NY, US); **HAITI.** GONAVE ISLAND: Anse Galette, *Leonard 3225* (NY); NORD: St. Michel de l'Atalye, *Leonard 7339* (MO, US); ARTIBONITE: Ennery-Rilboreau road, *Leonard 8831* (F, GH, UC, US); TORTUE ISLAND: La Vallée, *Leonard & Leonard 11328* (GH, MO, UC, US); **DOMINICAN REPUBLIC.** SANTIAGO: Hato del Yaque, Santiago, Valle de Cibao, *Ekman 16142* (A, B, F, G, GH, NY, US); SANTO DOMINGO: Santo Domingo, *Ekman 11417* (B, TEX, US); **PUERTO RICO.** Yauco, *Sintenis 3567* (G, GH, GOET, NY, US); Vieques Island, vicinity of Isabel Segunda, *Shafer 2415* (NY, US); Culebras Island, *Millspaugh 611* (F); **VIRGIN ISLANDS.** ST. CROIX: Granard Road, *Fosberg 54111* (US); ST. THOMAS: *Holton s.n.* (NY); VIRGIN GORDA: *Fishlock 190* (GH); TORTOLA: Paraquita Holding Ground, *D'Arcy 394* (A); **JAMAICA.** MIDDLESEX: Clarendon Parish W end of Round Hill, *Proctor 9470* (GH); SURREY: Kingston, *Britton & Hollich 1744* (NY); **CAYMAN ISLANDS.** CAYMAN BRAC: the creek, *Millspaugh 1167* (F, NY); GRAND CAYMAN: *Hitchcock s.n.* (MO); **ANGUILLA.** Crocus Bay, *Proctor 18585* (A, TEX); **ST. BERTHÉLEMY.** St. Jean, *Questel 242* (NY); **MARTINIQUE.** Grand Riviere, *Kimber 489* (WIS); **GRENADINES.** ISLE OF RONDE. *Howard 10722* (GH); GRENADA: Sport Lands, *W. 210* (A).

MEXICO. CAMPECHE: Campeche, *Perrine s.n.* (K, NY); QUINTANA ROO: Cozumel Island, *Lewis 6876* (MO, NY); TABASCO: 20 mi. N of Villahermosa, *Fryxell 733* (BH, F, MO, pf, UC); YUCATAN: *Valdez 22* (CAS, GH, K, MICH, MO, NY, US); Chichen Itzá, in clearing, *Steere 1010* (G, MICH, MO); CHIAPAS: San Cristóbal las Casas, *Breedlove 14065* (DS, pf); **BELIZE.** Corozal-St. Helena Rd., *Lundell 4825* (BH, MICH); **GUATEMALA.** PETÉN: Uaxactún, *Bartlett 12348* (MICH, US); Tikal Nat'l Park, Tikal, *Contreras 5588* (MICH, US); GUATEMALA: Finca Bretaña, road between Guatemala City and Fiscal, *Standley 59789* (F); QUICHÉ: near Sacapulas, *Standley 62503* (F); **EL SALVADOR.** SAN MIGUEL: Haciénda San Antonio, *Calderón 2129* (GH, US); **HONDURAS.** CORTES: banks of Río Chamelecón, road to Chamelecón, *Molina 11631* (F, NY, TEX); OLANCHO: trail between Catacamas and La Presa N of Catacamas, *Standley 18373* (F); TEGUCIGALPA: Morazán, near Suyapa, *Standley & Williams 1413* (F); EL PARAÍSO: Yuscarán, *Standley 25780* (F); YORO: Progreso, *Standley 55101* (US); **NICARAGUA.** ESTELÍ: 8 km. W of Estelí along Estanzuela Creek, *Molina 23070* (NY); 5 km. NW of Estelí, *Molina 27248* (F); **MANAGUA.** 12 km. E of Managua, *Seymour 6129* (NY); **GHANA.** *Hall s.n.* (srh).

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APPENDIX I.

Summary of *Malvastrum* distribution. Endemic taxa indicated by an asterisk (*).

NEW WORLD

UNITED STATES: *M. americanum* var. *americanum; M. aurantiacum**; *M. bicuspidatum* subsp. *bicuspidatum; M. corchorifolium; M. coromandelianum* subsp. *coromandelianum; M. hispidum**.

MEXICO: *M. americanum* var. *americanum; M. bicuspidatum* subsp. *bicuspidatum; M. bicuspidatum* subsp. *campanulatum**; *M. bicuspidatum* subsp. *oaxacanum**; *M. bicuspidatum* subsp. *tumidum* var. *tumidum**; *M. bicuspidatum* subsp. *tumidum* var. *glabrum**; *M. corchorifolium; M. coromandelianum* subsp. *coromandelianum*.

BELIZE: *M. americanum* var. *americanum* (possibly occurs); *M. corchorifolium; M. coromandelianum* subsp. *coromandelianum.*

GUATEMALA: *M. americanum* var. *americanum; M. corchorifolium; M. coromandelianum* subsp. *coromandelianum; M. guatemalense.*

EL SALVADOR: *M. americanum* var. *americanum; M. corchorifolium; M. coromandelianum* subsp. *coromandelianum.*

HONDURAS: *M. americanum* var. *americanum; M. corchorifolium; M. coromandelianum* subsp. *coromandelianum; M. guatemalense.*

NICARAGUA: *M. americanum* var. *americanum; M. corchorifolium; M. coromandelianum* subsp. *coromandelianum; M. guatemalense.*

COSTA RICA: *M. americanum* var. *americanum; M. coromandelianum* subsp. *coromandelianum.*

PANAMA: *M. americanum* var. *americanum; M. coromandelianum* subsp. *coromandelianum.*

CARIBBEAN ISLANDS: *M. americanum* var. *americanum; M. corchorifolium; M. coromandelianum* subsp. *coromandelianum.*

COLOMBIA: *M. americanum* var. *americanum; M. coromandelianum* subsp. *coromandelianum.*

VENEZUELA: *M. americanum* var. *americanum; M. coromandelianum* subsp. *coromandelianum; M. coromandelianum* subsp. *fryxellii; M. tomentosum.*

GUYANA: *M. coromandelianum* subsp. *coromandelianum.*

ECUADOR (incl. GALÁPAGOS): *M. americanum* var. *americanum; M. coromandelianum* subsp. *capitato-spicatum; M. coromandelianum* subsp. *coromandelianum; M. tomentosum* subsp. *tomentosum; M. tomentosum* subsp. *pautense**.

PERU: *M. americanum* var. *americanum; M. coromandelianum* subsp. *coromandelianum; M. scoparioides**; *M. tomentosum* subsp. *tomentosum.*

CHILE: *M. coromandelianum* subsp. *coromandelianum.*

BRAZIL: *M. americanum* var. *americanum; M. coromandelianum* subsp. *coromandelianum; M. coromandelianum* subsp. *fryxellii**; *M. tomentosum* subsp. *tomentosum.*

BOLIVIA: *M. amblyphyllum; M. americanum* var. *americanum; M. coromandelianum* subsp. *capitato-spicatum; M. coromandelianum* subsp. *coromandelianum; M. grandiflorum**; *M. interruptum; M. spiciflorum.*

PARAGUAY: *M. amblyphyllum; M. americanum* var. *americanum; M. coromandelianum* subsp. *capitato-spicatum* (possibly occurs);

M. coromandelianum subsp. *coromandelianum; M. tomentosum* (possibly occurs).

ARGENTINA: *M. amblyphyllum; M. americanum* var. *americanum; M. coromandelianum* subsp. *capitato-spicatum; M. coromandelianum* subsp. *coromandelianum; M. interruptum; M. spiciflorum.*

URUGUAY: *M. coromandelianum* subsp. *coromandelianum.*

OLD WORLD

AFRICA: *M. americanum* var. *americanum* (Cape Verde Islands); *M. corchorifolium* (Ghana); *M. coromandelianum* subsp. *coromandelianum* (Ghana, Kenya, Madagascar, Madeira, South Africa).

ASIA: *M. americanum* var. *americanum* (India, Burma, China (Fukien), Indonesian Archipelago (Timor)); *M. coromandelianum* subsp. *coromandelianum* (Oman, India, Sri Lanka, China, Taiwan, Viet Nam, Indonesia).

AUSTRALIA: *M. americanum* var. *americanum; M. americanum* var. *stellatum*; M. chillagoense*; M. coromandelianum* subsp. *coromandelianum.*

PACIFICA: *M. coromandelianum* subsp. *coromandelianum* (widespread).

APPENDIX II.

Data matrices used in the construction of the cladogram

I. OTU code

1 *Malvastrum hispidum* 2 *Malvastrum spiciflorum* 3 *Malvastrum interruptum* 4a *Malvastrum americanum* var. *americanum* 4b *Malvastrum americanum* var. *stellatum* 5 *Malvastrum chillagoense* 6a *Malvastrum tomentosum* subsp. *tomentosum* 6b *Malvastrum tomentosum* subsp. *pautense* 7 *Malvastrum scoparioides* 8 *Malvastrum guatemalense* 9a *Malvastrum bicuspidatum* subsp. *bicuspidatum* 9b *Malvastrum bicuspidatum* subsp. *campanulatum* 9c *Malvastrum bicuspidatum* subsp. *oaxacanum* 9d *Malvastrum bicuspidatum* subsp. *tumidum* var. *tumidum* 9e *Malvastrum bicuspidatum* subsp. *tumidum* var. *glabrum* 10 *Malvastrum grandiflorum* 11 *Malvastrum amblyphyllum* 12 *Malvastrum aurantiacum* 13a *Malvastrum coromandelianum* subsp. *coromandelianum*

13b *Malvastrum coromandelianum* subsp. *capitato-spicatum* 13c *Malvastrum coromandelianum* subsp. *fryxellii* 14 *Malvastrum corchorifolium*

II. Character code

1 Plants perennial (0) annual or perennial (0.5) or annual (1).
2 Plant height at maturity $\geqslant$ 1 m (0) or $<$ 1 m (1)
3 Stem-hairs stellate with 5–8 rays (0) lepidote (0.4) stellate with 2–5 rays (0.5) with 4 rays (0.6) mixed simple and stellate (1)
4 Stipules lanceolate (0) or narrowly lanceolate or subulate (1)
5 Petioles on midstem leaves $>$ 40 mm long (0) 20–40 mm (0.5) $<$ 20 mm (1)
6 Leaf-blades of midstem leaves 1.5–3.9 times longer than the petiole (0) or 4 or more times longer (1)
7 Leaf-blades of midstem leaves ovate (0) ovate-elliptic (0.5) or ovate-lanceolate to lanceolate (1)
8 Leaf-blades of midstem leaves usually lobed (0) occasionally lobed (0.5) or ovate-lanceolate to lanceolate (1)
9 Leaf-blade base cordate to truncate and broad (0) intermediate (0.5) or cuneate and narrow (1)
10 Leaf-blade apex acute or acuminate (0) or rounded (1)
11 Leaf-blade margin at midstem with 1.5–5 teeth/cm (0) or with $>$ 5 teeth/cm (1)
12 Leaf-blade of midstem leaves $\geqslant$ 8 cm long (0) or $<$ 8 cm long (1)
13 Leaf-blade of midstem leaves $\geqslant$ 6 cm wide (0) or $<$ 6 cm wide (1)
14 Leaf-blade adaxial surface hairs stellate with 5–8 rays (0) lepidote (0.4) stellate with 2–5 rays (0.5) with 4 rays (0.6) or simple only or mixed with a few stellate hairs with 2–4 rays (1)
15 Leaf-blade abaxial surface hairs stellate with 8–12 rays (0) mostly lepidote (0.4) stellate with 2–5 rays (0.5) with 4 rays (0.6) or simple only or mixed with a few stellate hairs with 2–4 rays (1)
16 Inflorescence at maturity of solitary axillary flowers (0) of basally leafy simple terminal racemes (0.5) of leafless axillary glomerate spicate racemes (0.6) or a terminal spike (1)

17 Bifid floral bracts absent (0) or present (1)
18 Pedicel at anthesis > 1 mm long (0) 0.5–1 mm long (0.5) or < 0.5 mm (1)
19 Bracteole width ≥ 1.0 mm (0) or < 1.0 mm (1)
20 Bracteole lanceolate to narrowly lanceolate (0) linear to filiform (0.5) or ovate (1)
21 Bracteole free from calyx (0) united < 2.0 mm to calyx (0.5) or united > 2 mm (1)
22 Sepals joined 0.3 times their length or less (0) or united 0.5 times or more (1)
23 Calyx-length in fruit 5–8 mm (0) or 9–20 mm (1)
24 Calyx-lobes in fruit erect (0) incurved (0.5) slightly spreading (0.8) or rotate (1)
25 Calyx-lobes triangular (0) intermediate (0.5) or deltate (1)
26 Calyx-lobes in fruit < 4 mm wide (0) or ≥ 4 mm (1)
27 Calyx abaxial surface-hairs stellate with 5–10 rays (0) lepidote (0.4) a mixture of simple and stellate with 2–8 rays usually different sizes (0.5) 2–4-rayed hairs mixed (1)
28 Petal-length 8–10 mm (0) more than 10 mm (0.5) or < 8 mm (1)
29 Petal-width ≥ 5 mm (0) < 5 mm (1)
30 Petals conspicuously cleft or emarginate (0) intermediate (0.5) or not conspicuously cleft or emarginate (1)
31 Petals yellow-orange (0) or paler (1)
32 Petals rotate (0) wide-campanulate (0.5) or campanulate (1)
33 Petals exceeding calyx by 3–8 mm (0) or by 0.0–2 mm (1)
34 Stamens 16–50 in number (0) 51–111 (0.5) or 5–15 (1)
35 Filament-tube 2.0–7.0 mm tall (0) or < 2.0 mm (1)
36 Filament-tube pubescent (0) or glabrous (1)
37 Pollen equatorial diameter ≤ 60 μm (0) 61–90 μm (0.5) or > 90 μm (1)
38 Pollen aperture number 4–7 (0) 8–20 (0.5) or > 20 (1)
39 Pollen-spine length 2–4 μm (0) or 5–10 μm (1)
40 Carpel number usually 9–12 (0) < 9 (0.5) > 12 (1)
41 Stigmas discoid to hemispherical (0) globose or subglobose (0.5) or unexpanded (1)
42 Stigmas exceeding anthers by 1.0–3.0 mm (0) or by 0.0–0.5 mm (1)
43 Styles not recurved at wilt (0) recurved at wilt (1)

44 Mericarp height including ornamentation 0.9 2.0 mm (0) or 2.5–6 mm (1)
45 Mericarp length including ornamentation 1.0–3 mm (0) or > 3 mm (1)
46 Proximal cusp absent (0) mucro only (0.5) present (1)
47 Proximal cusp length 0.0–0.5 mm (0) 0.5–1.0 mm (0.5) or 1–2.5 mm (1)
48 Distal cusps absent (0) or both present (1)
49 Distal cusps length 0 mm (0) 1–2 mm (0.5) or 0.1–1 mm (1)
50 Lateral faces smooth (0) slightly ribbed (0.5) or strongly ribbed (1)
51 Pericarpial lateral faces thin (0) intermediate or leathery (0.5) or firm and ligneous (1)
52 Distal margins not prolonged into a thin wing (0) slightly prolonged or rimmed (0.5) definitely prolonged (1)
53 Apical-distal-basal surface with conspicuous medial line (0) with inconspicuous line (0.5) or line absent (1)
54 Lateral faces at apical and distal margins glabrous (0) sparsely pubescent (0.5) or pubescent (1)
55 Vestiture of apical surface of stellate hairs (0) of asymmetrical or bilateral stellate hairs (0.3) of stellate and simple hairs mixed (0.5) of simple hairs only (0.6) or lacking (1)
56 Mericarp dehiscent (0) incompletely basally dehiscent (0.5) or indehiscent (1)
57 Endoglossum present (0) or absent (1)
58 Seed height 1.0–1.4 mm (0) or 1.5–3 mm (1)
59 Seed without apical-distal sulcus (0) with an inconspicuous sulcus (0.5) with sulcus (1)
60 Fruit-diameter including ornamentation 3.0–5 mm (0) 6–8 mm (0.5) or 9 11 mm (1)

RAW DATA MATRIX

Char.:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
OTU																				
1	1.0	1	0.5	1	1.0	0	1.0	1.0	1.0	0	0	1	1	0.5	0.5	0.0	0	0.0	1	0.5
2	0.0	0	0.0	1	0.5	0	0.0	0.5	0.0	0	0	1	1	0.5	0.0	0.6	0	0.0	1	0.5
3	0.0	0	0.6	1	0.5	0	0.0	1.0	0.0	0	0	0	1	0.5	0.0	0.6	1	0.0	1	0.5
4a	0.0	0	0.0	0	0.0	0	0.0	0.0	0.0	0	0	0	0	0.0	0.0	1.0	1	1.0	0	0.0
4b	0.0	0	0.0	0	1.0	0	1.0	0.5	0.0	0	0	1	1	0.0	0.0	1.0	1	1.0	0	0.0
5	0.0	1	0.0	1	1.0	0	0.0	1.0	0.0	0	0	1	1	0.0	0.0	0.5	1	0.0	1	0.5
6a	0.0	0	0.0	1	0.5	0	0.0	0.5	0.0	0	0	1	1	0.0	0.0	0.6	0	0.5	1	0.5
6b	0.0	0	0.0	1	0.5	0	0.0	0.5	0.0	0	0	1	1	0.0	0.0	0.6	0	0.5	1	0.5
7	0.0	0	0.0	1	0.0	0	0.0	0.5	0.0	0	0	0	0	0.0	0.0	0.5	1	0.5	1	0.5
8	0.0	0	1.0	1	0.0	0	0.5	1.0	0.5	0	0	1	1	1.0	0.0	0.5	1	0.0	0	0.0
9a	0.0	0	0.5	1	1.0	0	1.0	1.0	0.0	0	0	1	1	0.5	0.5	0.5	1	0.5	1	0.0
9b	0.0	0	0.0	1	1.0	1	1.0	1.0	0.0	0	0	1	1	0.0	0.0	0.5	1	0.5	0	0.0
9c	0.0	0	0.0	1	1.0	1	1.0	1.0	0.0	0	0	1	1	1.0	0.0	0.5	1	0.0	1	0.0
9d	0.0	0	0.0	1	0.5	0	0.5	1.0	0.5	0	0	1	1	1.0	1.0	0.5	1	0.0	0	0.0
9e	0.0	0	0.0	1	0.5	1	1.0	1.0	0.5	0	0	1	1	1.0	1.0	0.5	1	0.0	0	0.0
10	0.0	0	0.0	1	0.0	0	0.0	0.5	0.0	0	0	0	0	0.0	0.0	0.0	0	0.0	0	0.0
11	0.0	0	0.0	1	0.5	0	0.0	1.0	0.0	1	0	1	0	0.0	0.0	0.0	0	0.0	0	0.0
12	0.0	0	0.4	0	0.5	0	0.0	1.0	0.0	1	0	1	1	0.4	0.4	0.0	0	0.0	0	1.0
13a	0.5	1	0.6	0	1.0	0	1.0	0.5	0.5	0	0	1	1	1.0	1.0	0.0	0	0.0	0	0.0
13b	0.5	0	0.6	0	0.5	0	0.0	0.5	0.0	0	0	0	1	0.6	0.6	0.6	0	0.0	1	0.0
13c	0.5	0	1.0	0	1.0	0	0.0	1.0	0.0	0	1	1	1	1.0	1.0	0.5	1	0.5	1	0.0
14	0.5	0	0.6	0	0.5	0	0.0	1.0	0.0	0	0	1	1	0.6	0.5	1.0	1	0.5	1	0.0

RAW DATA MATRIX

Char.: / OTU	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
1	0.5	1	1	0.5	1.0	1	0.5	1.0	1	0.5	1	1.0	1	1.0	1	1	0.5	0.5	0	0.5
2	0.0	0	0	0.0	0.0	0	0.0	1.0	1	1.0	1	1.0	1	1.0	1	0	0.0	0.0	0	0.5
3	0.0	1	0	0.5	0.0	1	0.5	1.0	0	0.5	1	0.0	0	0.0	1	0	0.5	0.5	1	0.0
4a	0.5	0	1	0.5	0.5	1	0.5	0.0	0	0.0	0	0.0	0	0.0	0	0	0.0	0.5	0	1.0
4b	0.5	0	1	0.5	0.5	0	0.5	1.0	1	0.0	0	0.0	1	0.0	0	0	0.0	0.5	0	0.0
5	0.0	0	0	0.0	0.0	0	0.0	1.0	1	0.0	1	1.0	1	0.0	0	0	0.0	0.0	0	0.5
6a	0.0	0	0	1.0	0.5	1	0.0	1.0	0	0.0	0	0.0	0	0.0	0	0	0.0	0.5	0	0.0
6b	0.0	1	0	0.5	1.0	1	0.0	1.0	0	0.0	0	0.5	0	0.0	0	0	0.5	0.5	1	0.0
7	0.0	1	1	0.5	0.0	1	0.0	0.5	0	0.0	0	0.5	0	0.0	0	0	0.5	0.5	1	0.0
8	0.5	0	1	0.8	0.0	0	0.5	0.0	0	0.0	0	0.0	0	0.0	0	0	0.5	0.0	0	0.0
9a	0.5	1	1	1.0	0.5	1	0.5	0.0	0	0.0	0	0.0	0	0.0	0	0	0.0	0.0	0	0.0
9b	0.5	1	1	0.8	0.5	1	0.5	0.5	0	0.0	0	0.0	0	0.5	0	0	0.0	0.0	0	0.0
9c	0.5	0	1	0.8	0.0	1	0.5	0.5	0	0.0	0	0.0	0	0.0	0	0	0.5	0.0	0	0.0
9d	0.5	0	1	0.8	0.0	1	0.5	0.0	0	0.0	0	0.0	0	0.0	0	0	0.5	0.0	0	0.0
9e	0.5	0	1	0.8	0.0	0	0.5	0.0	0	0.0	0	0.5	0	0.0	0	0	0.5	0.0	0	0.0
10	0.5	0	1	0.0	0.0	1	0.5	0.5	0	0.5	0	0.5	0	0.5	0	0	1.0	1.0	1	1.0
11	0.5	0	1	0.0	1.0	1	0.0	0.0	0	0.0	1	1.0	1	0.0	0	0	0.5	1.0	1	1.0
12	1.0	1	1	1.0	1.0	1	0.4	0.5	0	0.0	0	0.0	0	0.0	0	1	1.0	0.5	1	1.0
13a	0.5	1	1	1.0	1.0	1	1.0	0.0	0	0.0	0	0.0	0	0.0	0	1	0.5	1.0	1	0.0
13b	0.5	1	0	0.5	1.0	1	1.0	0.0	0	0.0	1	0.0	0	0.0	1	1	0.5	0.5	1	0.0
13c	0.5	1	0	0.5	1.0	1	1.0	1.0	1	0.0	0	0.5	1	0.0	1	1	0.5	0.5	1	0.0
14	0.5	0	1	0.5	1.0	1	0.5	1.0	1	0.0	0	0.5	1	0.0	0	0	0.5	1.0	1	0.0

RAW DATA MATRIX

Char.:	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	Total Divergence Value (Σ character values)
OTU																					
1	0.5	1	1	1	1	0.0	0.0	0	0.0	0.0	0.5	0.0	0.0	1.0	0.6	0.0	1	1	0.0	0.5	36.6
2	0.0	1	1	0	0	0.5	0.0	0	0.0	0.5	0.0	0.0	0.5	0.0	0.0	1.0	1	0	0.0	0.0	20.6
3	0.0	0	1	0	0	0.5	0.0	0	0.0	0.0	0.0	0.0	1.0	0.5	0.3	1.0	1	1	0.0	0.0	22.5
4a	0.5	0	1	0	0	0.5	0.0	0	0.0	0.5	1.0	0.0	0.5	0.5	0.6	0.5	0	1	0.0	0.5	15.6
4b	0.0	1	0	0	0	0.5	0.0	0	0.0	0.5	1.0	0.0	0.5	0.5	0.5	1.0	0	0	0.0	0.0	19.5
5	1.0	1	1	0	0	0.0	0.0	0	0.0	1.0	1.0	0.0	0.0	0.5	0.6	1.0	1	0	0.0	0.0	22.6
6a	0.0	0	1	1	1	1.0	0.0	1	0.5	1.0	1.0	0.0	0.0	1.0	0.0	1.0	0	1	1.0	0.5	22.6
6b	0.5	0	1	1	0	1.0	0.0	1	1.0	0.5	1.0	0.0	0.5	1.0	0.3	1.0	0	1	0.0	0.5	24.9
7	0.0	0	0	1	1	1.0	0.0	1	1.0	0.5	1.0	0.5	0.0	0.5	0.5	1.0	0	1	0.0	0.5	22.0
8	0.0	0	1	0	0	0.0	0.0	1	1.0	0.5	1.0	0.0	0.5	1.0	0.5	1.0	1	1	1.0	0.0	22.3
9a	0.5	0	1	0	1	0.0	0.0	1	0.5	1.0	1.0	0.0	0.5	0.5	0.5	1.0	1	1	1.0	0.5	28.0
9b	0.0	1	1	0	1	0.0	0.0	1	1.0	0.5	1.0	0.0	0.5	0.5	0.5	1.0	1	1	0.5	0.5	27.3
9c	0.5	0	1	0	0	0.0	0.0	1	1.0	0.5	0.5	0.5	0.0	0.0	0.0	1.0	0	1	0.0	0.5	22.8
9d	0.0	0	1	0	0	0.0	0.0	1	1.0	0.0	0.5	0.0	0.0	0.0	0.5	1.0	1	1	0.5	0.5	21.3
9e	0.0	0	1	0	0	0.0	0.0	1	1.0	0.0	0.5	0.0	0.0	0.0	1.0	1.0	1	1	0.5	0.0	22.3
10	0.5	0	0	1	1	1.0	0.5	1	0.5	1.0	1.0	1.0	0.0	0.0	0.6	1.0	1	1	0.0	0.5	23.1
11	0.5	1	0	1	1	1.0	0.5	1	1.0	1.0	1.0	1.0	0.0	0.0	0.6	1.0	1	1	0.0	1.0	29.1
12	0.5	0	1	1	1	1.0	1.0	1	0.5	0.0	1.0	0.0	0.5	0.5	0.5	1.0	1	1	0.0	1.0	31.6
13a	0.5	0	1	1	1	1.0	1.0	1	1.0	1.0	1.0	0.5	0.5	0.5	0.5	1.0	1	1	0.0	0.5	34.1
13b	0.5	1	1	1	1	1.0	1.0	1	1.0	1.0	1.0	0.5	0.5	0.5	0.5	1.0	1	1	0.0	0.5	31.9
13c	0.5	0	1	0	0	1.0	0.5	1	1.0	0.5	1.0	0.5	0.5	0.5	0.6	1.0	1	0	0.0	0.0	34.6
14	0.5	1	1	1	0	1.0	0.0	1	1.0	1.0	1.0	0.0	0.5	1.0	0.5	0.5	0	1	0.0	0.5	32.3

DISTANCE MATRIX

OTU	1	2	3	4a	4b	5	6a	6b	7	8	9a	9b	9c	9d	9e	10	11	12	13a	13b	13c	14
1	0	31	31	40	38	30	38	34	41	40	32	38	35	36	38	39	35	37	34	34	36	32
2		0	23	36	26	16	28	29	38	33	38	36	34	34	34	39	35	43	47	38	37	38
3			0	29	29	30	28	23	27	29	30	34	30	27	30	35	38	33	37	27	31	33
4a				0	15	32	28	27	27	26	25	25	26	28	32	27	32	32	34	33	34	27
4b					0	24	27	28	30	23	25	22	26	28	28	37	37	35	33	37	28	26
5						0	28	31	33	29	30	30	29	31	25	37	30	41	42	40	33	34
6a							0	13	20	29	22	26	27	28	33	27	30	29	32	29	36	28
6b								0	15	29	28	27	29	30	32	29	28	27	28	23	25	20
7									0	29	28	25	27	29	32	22	28	30	30	27	30	28
8										0	19	18	16	9	11	33	33	33	28	35	31	29
9a											0	13	20	20	24	34	34	27	24	31	30	27
9b												0	16	18	19	31	33	31	29	33	33	30
9c													0	13	14	29	31	35	29	34	29	28
9d														0	6	31	30	32	27	34	34	29
9e															0	33	32	36	31	39	33	32
10																0	16	27	29	33	39	33
11																	0	26	28	28	35	28
12																		0	21	24	32	31
13a																			0	15	25	26
13b																				0	23	23
13c																					0	23
14																						0

APPENDIX III.

A *MALVASTRUM* NOMENCLATOR (EXCLUDED or UNCERTAIN SPECIES)

Summary of names published in *Malvastrum* and their present taxonomic placement. An asterisk (*) precedes the currently accepted name. To avoid repetition cross references are made to names treated previously in the text. New names published after 1979 are excluded from this list but are included in the text.

Malvastrum abbottii Eastwood, Leafl. W. Bot. **1:** 215. 1936. TYPE: California: Monterey Co., Salinas River, *Abbott s.n.* (Holotype: CAS no. *52708;* isotypes: CAS, GH). **Malacothamnus abbottii* (Eastw.) Kearney, Leafl. W. Bot. **6:** 129. 1951.

M. aboriginum Robinson in A. Gray, Syn. Fl. N. Am. **1,** 1: 311. 1897. TYPE: California: Monterey Co., Indian Valley near the Salinas River, *Curran s.n.* (Holotype: CAS no. *741*). **Malacothamnus aboriginus* (Robins.) Greene, Leafl. Bot. Observ. Crit. **1:** 208. 1906.

M. acaule (Dombey ex Cavanilles) A. Gray. U. St. Expl. Exped. 1: 150, *in adn.* 1854. Basionym: *Malva acaulis* Dombey ex Cavanilles, Diss. **2:** 82, t. 35, f. 2. 1786. TYPE: Peru: Dep. Lima, Cordillera, *Dombey 677* (Holotype: P; isotype: G, K, MA). **Acaulimalva acaulis* (Dombey ex Cav.) Krap. Darwiniana **19:** 15. 1974.

M. acaule var. *granatense* (Weddell) E. G. Baker, J. Bot. **29:** 171 (new comb. not indicated). 1891. Basionym: *Malva acaulis* var. *β granatensis* Weddell, Chlor. And. **2:** 275. 1861. TYPE: Venezuela: Prov. Mérida, Páramo de Machuchies, alt. 3900 m, *Linden 1425* (Lectotype: P; isotype: G! OXF!) **Acaulimalva purdiaei* (A. Gray) Krap., Darwiniana **19:** 26. 1974.

M. albens Harvey in Harvey & Sonder, Fl. Cap. **1:** 163. 1860. TYPE: South Africa: Cape Province, Malmesbury Distr., Riebeckskasteel, hills under 1000 ft., *Drege s.n.* (Lectotype: K; isotypes: BM, G, K, L, MO, P). **Anisodontea biflora* (Desrousseaux) Bates, Gentes Herb. **10:** 340. 1969.

M. albertii (Philippi) K. Reiche, Anales Univ. Chile **91:** 379. 1895 ("*alberti*"). Basionym: **Tarasa albertii* Philippi, Anales Univ. Chile **82:** 321. 1893 ("*Tarassa Alberti*"). TYPE: Argentina: Prov.

Mendoza (Colchagua), Portezuelo del Tinguiririca, Valle de Sasneado, *Albert s.n.* (Holotype: SGO no. *52169*).

M. alexandri E.G. Baker, J. Bot. **29:** 166. 1891. TYPE: South Africa: Cape Province, George District, *Alexander s.n.* (Holotype: BM, fragment at K). **Anisodontea alexandri* (E. G. Baker) Bates, Gentes Herb. **10:** 336. 1969.

M. alexandri sensu Hutchinson, Bot. in S. Afr. 79, 80, f. p. 81. 1946, non E.G. Baker, 1891. **Anisodontea setosa* (Harvey) Bates, Gentes Herb. **10:** 344. 1969.

M. alismatifolium K. Schumann & Hieronymus, Bot. Jahrb. Syst. **21:** 318. 1896. TYPE: Peru: Dep. Cajamarca. Puna desert near Centimal and Comullca between Pacasmayo and Moyobamba, *Stübel 39* (Holotype: B (lost) — photo Field museum ser. no. *9306* at F!, fragment of holotype at K! (mericarps)). **Acaulimalva alismatifolia* (K. Schum. & Hieron.) Krap., Darwiniana **19:** 16. 1974.

**M. amblyphyllum* R. E. Fries. *See text.*

**M. americanum* (Linnaeus) Torrey in Emory. *See text.*

M. angustifolium (Cavanilles) Hemsley, Biol. Centr. Am. Bot. **1:** 99. 1879. Basionym: *Malva angustifolia* Cavanilles, Diss. **2:** 64, t. 20, f. 3. 1786. TYPE: Mexico. Cultivated at the Royal Botanic Garden, Madrid, seeds from Palau (Holotype: MA; isotype: MA). **Sphaeralcea angustifolia* (Cav.) G. Don, Hist. Dichl. Pl. **1:** 465. 1831.

M. angustifolium (Harvey) Stapf ex Fourcade, Bot. Surv. S. Afr. Mem. **20:** 56. 1941, non Hemsley, 1879. Basionym: *Malvastrum virgatum* (Murr.) Gray & Harvey in Harvey & Sonder var. *β angustifolium* Harvey in Harvey & Sonder, Fl. Cap. **1:** 162. 1860 ("*angustifolia*"). TYPE: South Africa: *Drège 7320* (Lectotype: K; isotypes: G!, L, MO, P, S). **Anisodontea scabrosa* (L.) Bates, Gentes Herb. **10:** 368. 1969.

M. angustum A. Gray. **Malvastrum hispidum* (Pursh) Hochreutiner. *See text.*

M. anthemidifolium (Remy) A. Gray, Bot. U. St. Expl. Exped. **1:** 152, *in adn.* 1854. Basionym: *Sida anthemidifolia* J. Remy, Ann. Sci. Nat. Bot. ser. 3, **6:** 356. 1846. TYPE: Bolivia: Alto de Tola, road from Potosí to Oruro, *D'Orbigny 1357* (Lectotype: P). **Nototriche anthemidifolia* (Remy) A. W. Hill, Bot. Jahrb. Syst. **37:** 578. 1906.

M. antofagastanum E. G. Baker, J. Bot. **29:** 167. 1891. First published as a nomen nudum in J. Bot. **28:** 368. 1890, based upon the label name *Malva antofagastana* Philippi, later published by Philippi in Anales Mus. Nac. Chile Bot. **2:** 7. 1891. TYPE: Argentina: Prov. Catamarca. Antofagasta de la Sierra, alt. 3570 m, *Philippi s.n.* (Holotype: K; isotypes: B (lost)—photo Field Mus. ser. no. *9307* at F!, SGO nos. *41034* and *51991).* **Tarasa antofagastana* (Phil.) Krap., Bol. Soc. Argent. Bot. **5:** 130. 1954.

M. arcuatum (Greene) Robinson in A. Gray, Syn. Fl. N. Am. 1, **1:** 311. 1897. Basionym: *Malveopsis arcuata* Greene, Man. Bot. San Franc. Bay: 66. 1894. TYPE: California: San Mateo Co., eastern slopes of the coast range back of Belmont, *Greene s.n.* (Holotype: UC no. *191563*). **Malacothamnus arcuatus* (Greene) Greene, Leafl. Bot. Observ. Crit. **1:** 208. 1906.

M. arequipense I. M. Johnston, Contr. Gray Herb. n.s. **70:** 74. 1924. TYPE: Peru: Dep. Arequipa. Hillside on the south slope of Chachani Mountain near Arequipa, alt. 2100 m, *Hinkley & Hinkley 43a* (Holotype: GH). **Urocarpidium albiflorum* Ulbrich, Bot. Jahrb. Beibl. **117:** 64. 1916.

M. aretioides A. Gray, Bot. U. St. Expl. Exped. **1:** 153. 1854. TYPE: Peru: Dep. Lima. Cordilleras at Casa Cancha, *Pickering s.n.* (Holotype: US!) **Nototriche aretioides* (A. Gray) A. W. Hill, Bot. Jahrb. Syst. **37:** 579. 1906.

M. asperrimum (Jacquin) Gray & Harvey in Harvey & Sonder, Fl. Cap. **1:** 161. 1860. Basionym: *Malva asperrima* Jacquin, Hort. Schoenbr. **2:** 7, t. 139. 1797. TYPE: t. 139, chosen by Bates (1969) is the lectotype. **Anisodontea bryoniifolia* (L.) Bates, Gentes Herb. **10:** 353. 1969.

M. asperrimum var. *β stellatum* (Thunberg) Harvey in Harvey & Sonder, Fl. Cap. **1:** 161. 1860. Basionym: *Malva stellata* Thunberg, Prodr. Pl. Cap.: 119. 1800. TYPE: South Africa: *Thunberg s.n.* (Holotype: UPS — Microfiche number *16012*). **Anisodontea bryoniifolia* (L.) Bates, Gentes Herb. **10:** 353. 1969.

**M. aurantiacum* (Scheele) Walpers. *See text.*

M. auricomum Philippi, Anales Mus. Nac. Chile Bot. **2:** 8. 1891. Also Philippi ex E. G. Baker, J. Bot. **29:** 365. 1891. TYPE: Chile: Atacama Desert, between Machuca and Copacoya, alt. 1130 m, *Philippi 1819* (Holotype: SGO no. *41051;* isotype: SGO no. *51993,*

K). **Nototriche auricoma* (Philippi) A. W. Hill, Bot. Jahrb Syst. **37:** 579. 1906.

M. bakerianum A. W. Hill, J. Linn. Soc. Bot. **39:** 228. 1909. TYPE: Peru: Dep. Puno, Tirapata, between Pucara and Ayauiri, alt. 12,730 ft., *Hill 74* (Lectotype: K!). **Acaulimalva engleriana* (Ulbr.) Krap., Darwiniana **19:** 19. 1974.

M. bakerianum f. *hirsutissimum* R. E. Fries, Kongl. Svenska Vetenskapsakad. Handl. **24:** 12. 1947. TYPE: Peru: Dep. Puno, Chuquibambilla, *Pennell 13417, pro parte,* (Holotype: S!; isotypes: F!, K!, PH!). **Acaulimalva engleriana* (Ulbr.) Krap., Darwiniana **19:** 19. 1974.

M. bakerianum var. *strigosum* A. W. Hill, Kew Bull.: 160. 1935. TYPE: Peru: Dep. Cuzco. high valley, Urcos, alt. 3600–4800 m., *Stafford 325* (Lectotype: K!; isotype: K!, US) **Acaulimalva engleriana* (Ulbr.) Krap., Darwiniana **19:** 19. 1974.

M. belloum (Gay) E. G. Baker, J. Bot. **28:** 368. 1890. Combination often incorrectly attributed to Gray (1854). Basionym: *Malva belloa* Gay, Fl. Chil. **1,** 3: 304, t. 7. 1846. TYPE: Chile: Prov. Coquimbo. Hautenlauque near the ocean, río Huapo, *Gay 801* (Holotype: P; isotypes: B (lost) — photo Field Mus. ser. no. 9308 — F!, F!, G!, K, P). **Sphaeralcea purpurata* (Lindley) Krap., Lilloa **17:** 218. 1949.

M. betonicifolium A. W. Hill, J. Linn. Soc. Bot. **39:** 221. 1909. ("*betonicaefolium*"). TYPE: Peru: Dep. Ayacucho, Andes of Huanta, alt. 3950–4260 m, *Pearce s.n.* (Holotype: K). **Acaulimalva betonicifolia* (A. W. Hill) Krap., Darwiniana **19:** 16. 1974 ("*betonicaefolia*"). See also *M. purdiei* var. *huantense.*

**M. bicuspidatum* (S. Watson) Rose. *See text* for additional information on this and new subspecific taxa.

M. bolivianum E. G. Baker, J. Bot. **29:** 168. 1891. TYPE: Bolivia: Prov. Tarija. Tarija, *Pearce s.n.* (Holotype: K). **Tarasa heterophylla* (Griseb.) Krap., Bol. Soc. Argent. Bot. **5:** 124. 1954.

M. borussicum (Meyen) Weddell, Chlor. And. **2:** 278. 1861. Basionym: *Sida borussica* Meyen, Reise **2:** 31. 1834. TYPE: Peru: near Lake Titicaca, plateau, *Meyen s.n.* (Holotype: B (lost)). **Nototriche borussica* (Meyen) A. W. Hill, Bot. Jahrb. Syst. **37:** 579. 1906.

M. bryoniifolium (Linnaeus) Gray & Harvey in Harvey & Sonder, Fl. Cap. **1:** 161. 1860. ("*bryonifolium*"). Basionym: *Malva bry-*

oniifolia Linnaeus, Sp. Pl. **2:** 688. 1753 ("*bryonifolia*"). TYPE: in Linnaean Herbarium (Lectotype: LINN *870. 7*—chosen by Bates (1969)). **Anisodontea bryonifolia* (L.) Bates, Gentes Herb. **10:** 353. 1969.

M. buchtienii Pax ex Lingelsheim, Pax & Winkler, Feddes Repert. Spec. Nov. Regni Veg. **7:** 243. 1909. TYPE: Bolivia: Prov. La Paz. High plateau near Viacha, 30 km S of La Paz, alt. 3900 m, *Buchtien 928* (Holotype: B (lost)—photo Field mus. ser. no. *9309;* isotype: K!, NY!, US!). **Acaulimalva nubigena* (Walp.) Krap., Darwiniana **19:** 22. 1974.

M. bullatum Ekman, Ark. Bot. **13:** 6, t. 1, f. 1. 1914. TYPE: Brazil: Est. Paraná. High plateau, Calmão, *Dusén 9331* (Holotype: s!; isotype: F!). **Monteiroa bullata* (Ekman) Krap., Bol. Soc. Argent. Bot. **3:** 242. 1951.

M. burchellii E. G. Baker, J. Bot. **29:** 165. 1891. TYPE: South Africa: Cape Province. Near the mouth of the Knysna River near Melkhout Kraal, *Burchell 5386* (Holotype: K; isotypes: GH, L). **Anisodontea scabrosa* (L.) Bates, Gentes Herb. **10:** 368. 1969.

M. calycinum (Cavanilles) Gray & Harvey in Harvey & Sonder, Fl. Cap. **1:** 161. 1860. Basionym: *Malva calycina* Cavanilles, Diss. **2:** 81, t. 22, f. 4. 1786. TYPE: South Africa. Cape Province. Cape of Good Hope, *Thunberg s.n.* (Lectotype: MA; isotype: UPS - microfiche no. *15967). *Anisodontea scabrosa* (L.) Bates, Gentes Herb. **10:** 368. 1969.

M. campanulatum (Paxton) Nicholson, Dict. Gard. **2:** 319. 1885. Basionym: *Malva campanulata* Paxton, Paxton's Mag. Bot. **9:** 173, f. p. 172. 1843. TYPE: Described from specimens at Henderson's Nursery apparently unvouchered. A specimen at Kew (photo, Muñoz Pizarro neg. no. *1625* — srh!) grown there in 1855 is certainly this plant and may be from the same line. (Lectotype: the figure, p. 172, is chosen as lectotype). **Sphaeralcea purpurata* (Lindl.) Krap., Lilloa **17:** 218. 1949.

M. capense (Linnaeus) Gray & Harvey in Harvey & Sonder, Fl. Cap. **1:** 160, 1860, quoad basionym. Basionym: *Malva capensis* Linnaeus, Sp. Pl. **2:** 688. 1753. TYPE: a cultivated specimen from the Clifford estate (Holotype: BM Clifford Herbarium). **Anisodontea capensis* (L.) Bates, Gentes Herb. **10:** 327. 1969.

M. capense sensu Gray & Harvey in Harvey & Sonder, Fl. Cap. **1:** 160. 1860, excl. basionym. **Anisodontea scabrosa* (L.) Bates, Gentes Herb. **10:** 368. 1969.

M. capense var. *β balsamicum* (Jacquin) Harvey in Harvey & Sonder, Fl. Cap. **1:** 160. 1860. Basionym: *Malva balsamica* Jacquin, Misc. Austr. **2:** 321. 1781; Ic. Pl. Rar. **1,** 1: t. 140. 1781. TYPE: t. 140, chosen by Bates (1969), is the lectotype. **Anisodontea scabrosa* (L.) Bates, Gentes Herb. **10:** 368. 1969.

M. capense var. *fragrans* (Jacquin) E. G. Baker, J. Bot. **29:** 164. 1891. Basionym: *Malva fragrans* Jacquin, Horti. Bot. Vindobon. **3:** 20, t. 33. 1776. TYPE: t. 33, chosen by Bates (1969), is the lectotype. **Anisodontea scabrosa* (L.) Bates, Gentes Herb. **10:** 368. 1969.

M. capense var. *α glabrescens* Harvey in Harvey & Sonder, Fl. Cap. **1:** 160. 1860, quoad basionym. TYPE: As for *Malva capensis* L., see *M. capense* above and Bates (1969). **Anisodontea capensis* (L.) Bates.

M. capense var. *α glabrescens* sensu Harvey in Harvey & Sonder, Fl. Cap. **1:** 160. 1860, excl. basionym. **Anisodontea scabrosa* (L.) Bates, Gentes Herb. **10:** 368. 1969.

M. capitatum (Cavanilles) Grisebach, Abh. Königl. Ges. Wiss. Göttingen **19:** 90. 1874. Basionym: *Malva capitata* Cavanilles, Diss. **5:** 280, t. 137, f. 1. 1788. TYPE: Peru: Colonia Sacramento y Montevideo, *Neé s.n.* (Holotype: MA – photo no. *29769* at F!; isotype: C!, F!). **Tarasa capitata* (Cav.) Bates, Gentes Herb. **9:** 388. 1965.

M. carpinifolium A. Gray. **M. coromandelianum* (L.) Garcke. *See text.*

M. casabambense Stuckert, Anales Soc. Ci. Argent. **114:** 24. 1932. TYPE: Argentina: Prov. Córdoba, Casa Bamba, *Stuckert 23518.* (Neotype: CORD; isotype: BAA – photo srh!). Krapovickas (pers. comm.) has not been able to find the specimen dated 'XI, 1927' cited by Stuckert, but has discovered *Stuckert 23518,* collected in 1930-1931 at Casa Bamba and annotated with this name by Stuckert, in the Stuckert Herbarium (CORD) and in the Parodi Herbarium (BAA). The plant is **Melochia argentina* R. E. Fries, Meded. Rijk. Herb. Leid. **19:** 42. 1913.

M. castelnauianum Weddell, Chlor. And. **2:** 283, t. 80, f. A, 1861 ("*castelnaeanum*"). TYPE: Peru: Dep. Cuzco, Cordilleras of Cuzco, *de Castelnau s.n.* (Lectotype: P). **Nototriche castelnauiana* (Wedd.) A. W. Hill, Bot. Jahrb. Syst. **37:** 579. 1906 ("*castelnaeana*").

M. catalinense Eastwood, Leafl. W. Bot. **1:** 215. 1936. TYPE: California: Santa Catalina Island, *Eastwood 6442* (Holotype: CAS no. *52692*). **Malacothamnus fasciculatus* (Nutt. ex Torr. & Gray) Greene subsp. *catalinensis* (Eastw.) R. F. Thorne, Aliso **6:** 55. 1967.

M. catamarcense I. M. Johnston, Contr. Gray Herb. n.s. **70:** 75. 1924. TYPE: Argentina: Prov. Catamarca. El Candado, Dep. Andalgalá, *Jörgensen 1388* (Holotype: GH! isotypes: MO!,US!). **Urocarpidium pentandrum* (K. Schum.) Krap., Darwiniana **10:** 632. 1954.

M. cavanillesii A. Gray, Bot. U. St. Expl. Exped. **1:** 156. 1854. Based upon: *Sida acaulis* Cavanilles, Ic. Pl. **5:** 13, t. 422, f. 2. 1799. TYPE: (Holotype: MA—photo srh!; isotype: MA). **Nototriche acaulis* (Cav.) Krap., Bol. Soc. Argent. Bot. **15:** 286. 1973.

**M. chillagoense* K. Domin. *See text.*

M. clandestinum (Phil.) E. G. Baker, J. Bot. **29:** 363. 1891. Basionym: *Sida clandestina* Philippi, Flor. Atac.: **11.** 1860. TYPE: Chile: Atacama Desert, Valle Sandón, Lat. 25° 4′ S, alt. 2,743 m, *Philippi s.n.* (Holotype: SGO No. *51994;* isotypes: B (lost), SGO No. *41064).* **Nototriche clandestina* (Phil.) A. W. Hill, Bot. Jahrb. Syst. **37:** 579. 1906.

M. clementinum Munz & I. M. Johnston, Bull. Torrey Bot. Club **51:** 296. 1924. TYPE: California: Los Angeles Co., San Clemente Island, canyon walls near Lemon Tank, *Munz 6684* (Holotype: POM no. *20491;* isotypes: CAS, F!, GH!, NY, US!). **Malacothamnus clementinus* (Munz & I. M. Johnston) Kearney, Leafl. W. Bot. **6:** 127. 1951.

M. coccineum (Nuttall) A. Gray var. *coccineum,* Mem. Amer. Acad. Arts. n.s. **4:** 21, in adn. 1849. Basionym: *Malva coccinea* Nuttall, Fraser's Catalogue: 2. 1813. TYPE: "from the river Platte to the Rocky Mountains", *Nuttall s.n.* (Lectotype: PH!; isotypes: OXF!, PH!). **Sphaeralcea coccinea* (Nutt.) Rydberg var. *coccinea,* Bull. Torrey Bot. Club **40:** 58. 1913. See Southwestern Naturalist **23:** 657. 1978 for information on this species.

M. coccineum var. *β dissectum* (Nuttall in Torrey & Gray) A. Gray, Mem. Amer. Acad. Arts, n.s. **4:** 24. 1849. Basionym: *Sida dissecta* Nuttall in Torrey & Gray, Fl. N. Am. **1:** 235. 1838. TYPE: Plains of the Upper Platte River, *Nuttall s.n.* (Lectotype: BM: isotype: PH). **Sphaeralcea coccinea* (Nutt.) Rydb. var. *coccinea,* Bull. Torrey Bot. Club **40:** 58. 1913.

M. coccineum var. *elatum* E. G. Baker, J. Bot. **29:** 171. 1891. TYPE: Western Texas to El Paso, *Wright 41* (Lectotype: BM; isotypes: G!, GH!, MO, NY, OXF!, US!). **Sphaeralcea coccinea* (Nutt.) Rydb. var. *elata* (E. G. Baker) Kearney in Kearney & Peebles, J. Wash. Acad. Sci. **29:** 486. 1939.

M. coccineum var. *grossulariifolium* (Hook & Arn.) Torrey in Stansbury, Bot. Stansb. Exped.: 384. 1852. ("*grossulariaefolium*"). Basionym: *Sida grossulariifolia* Hooker & Arnott, Bot. Beechey Voy.: 326. 1838 ("*grossulariaefolia*"). TYPE: "Bamcock River, Snake Country", prob. Bannock River, Power Co., Idaho, collector not indicated (Holotype: K; isotype: Y). **Sphaeralcea grossulariifolia* (Hook & Arn.) Rydberg, Bull. Torrey Bot. Club **40:** 48. 1913 ("*grossulariaefolia*").

M. cockerellii A. Nelson, Bot. Gaz. (Crawfordsville) **34:** 24. 1902 *("cockerelli").* Based upon *Sida dissecta* Nutt. in Torr. & Gray, see *M. coccineum* var. *dissectum* above. **Sphaeralcea coccinea* (Nutt.) Rydb. var. *coccinea.*

M. compactum (Gay) A. Gray, Bot. U. St. Expl. Exped. **1:** 152, *in adn.* 1854. Basionym: *Sida compacta* Gay, Fl. Chil. **1:** 329. 1846, non St.-Hil & Naud, 1842. TYPE: Chile: Prov. Santiago, Cordillera of Santiago, alt. 3100 m, *Gay s.n.* (Lectotype: P (no. *894,* prob. not Gay's number); isotypes: B!, F!, K, P). **Nototriche compacta* (Gay) A. W. Hill, Bot. Jahrb. Syst. **37:** 579. 1906.

M. condensatum E. G. Baker, J. Bot. **29:** 363. 1891. TYPE: Peru: Dep. Puno, near Ayapata, *Lechler 1972* (Holotype: K; isotype: P). **Nototriche condensata* (E. G. Baker) A. W. Hill, Bot. Jahrb. Syst. **37:** 579. 1906.

M. confertum Parish ex Jepson, Man. Fl. Pl. Calif.: 631. 1925, pro syn., nomen nudum. Based on *Parish 3786* June 25, 1890, San Bernardino Co., California (DS?). **Sidalcea hickmanii* Greene var. *parishii* Robinson in Gray, Syn. Fl. N. Amer. **1,** 1: 307. 1897.

M. congestiflorum I. M. Johnston, Contr. Gray Herb. **70:** 74. 1924. TYPE: Peru: Dep. Arequipa. South slope of Chachani Mountain near Arequipa, alt. 2745 m, *Hinkley & Hinkley 37* (Holotype: GH). **Tarasa congestiflora* (I. M. Johnst.) Krap., Bol. Soc. Argent. Bot. **5:** 138. 1954.

M. conglomeratum Grisebach ex K. Schumann in Martius, Fl. Bras. **12,** 3: 273, 1891, nomen nudum. Presumably an orthographic error for *Malvastrum glomeratum* (Hook & Arn.) Griesbach,

Abh. Königl. Ges. Wiss. Göttingen **24:** 42. 1879. See *M. glomerata.* **Monteiroa glomerata* (Hook & Arn.) Krap.

M. copelandii Hieronymus, Bot. Jahrb. Syst. 20 Beibl. **49:** 43. 1895. TYPE: Peru: near Vincocaya, alt. 4376 m, *Copeland s.n.* (Holotype: B (lost)). **Nototriche orbignyana* (Weddell) A. W. Hill, Bot. Jahrb. Syst. **37:** 579. 1906.

**M. corchorifolium* (Desrousseaux) Britton ex Small. *See text.*

M. cordifolium N. Rojas-Acosta, Cat. Hist. Nat. Corrient.: 53. 1897. Krapovickas (pers. comm.) considers this a possible synonym of *Sida cordifolia* L. The publication is very scarce and has not been examined, and most of the species in the work have not been evaluated.

**M. coromandelianum* (Linnaeus) Garcke subsp. *coromandelianum. See text.*

M. coromandelianum f. *breviaristata* Chodat & Hassler. **Malvastrum coromandelianum* (L.) Garcke subsp. *coromandelianum. See text.*

M. coromandelianum var. *congestum* R. E. Fries. **Malvastrum coromandelianum* (L.) Garcke subsp. *capitato-spicatum* (O. Kuntze) S. R. Hill. *See text.*

M. corymbosum Sandwith, Kew Bull.: 174. 1927. TYPE: Argentina: Prov. Neuquén. Rio Coyunco, *Comber 140* (Holotype: K). **Tarasa albertii* Philippi, Anales Univ. Chile **82:** 321. 1893.

M. coulteri S. Watson, Proc. Amer. Acad. Arts **11:** 125. 1876. TYPE: California: southeastern region (?), *Coulter 96* (Lectotype: GH — presence not verified). **Sphaeralcea coulteri* (S. Watson) A. Gray, Proc. Amer. Acad. Arts **22:** 291, *in adn.* 1887.

M. crenatum A. W. Hill, J. Linn. Soc. Bot. **39:** 227. 1909. TYPE: Peru: Dep. Lima. Hacienda Arapa, near Yauli, Lima-Oroya RR, alt. 4400 m, *Weberbauer 360* (Holotype: B (lost) — photo Field Mus. ser. no. *9311* at F! fragment of holotype K!; isotype: G). **Acaulimalva crenata* (A. W. Hill) Krap., Darwiniana **19:** 18. 1974.

M. crozophoroides Stapf ex Hutchinson, Botanist in S. Afr.: 436. 1946, sine descr. lat. Invalidly published. **Anisodontea malvastroides* (E. G. Baker) Bates, Gentes Herb. **10:** 314. 1969.

M. davidsonii Robinson in A. Gray, Syn. Fl. N. Am. **1,** 1: 312. 1897. TYPE: California: Los Angeles Co., San Fernando Valley, *Davidson s.n.* (Lectotype: GH; isotype: ND, US!). **Malacotham-*

nus davidsonii (Robinson) Greene, Leafl. Bot. Observ. Crit. **1:** 208. 1906.

M. decipiens (St.-Hil. & Naud.) K. Schumann in Martius, Fl. Bras. **12,** 3: 275. 1891. Basionym: *Sida decipiens* Saint-Hilaire & Naudin, Ann. Sci. Nat. Bot. **2:** 54. 1842. TYPE: Brazil: Est. Rio Grande do Sul, *St.-Hilaire s.n.* (Holotype: P). **Sphaeralcea decipiens* (St.-Hil. & Naud.) Krap., Lilloa **17:** 216. 1949.

M. deflexum (Turczaninow) Stapf ex Fourcade, Bot. Surv. S. Afr. Mem. **20:** 56. 1941. Basionym: *Malva deflexa* Turczaninow, Bull. Soc. Imp. Naturalistes Moscou **31:** 186. 1858. TYPE: South Africa: Karro desert near the Gauritzrivier towards Graafreynet, *Ecklon & Zeyher 284* (Holotype: LE; isotypes: C, G!, K, L, MO, NBG, OXF!, P, S). **Anisodontea triloba* (Thunb.) Bates, Gentes Herb. **10:** 363. 1969.

M. densiflorum S. Watson, Proc. Amer. Acad. Arts **17:** 368. 1882. TYPE: California: San Diego Co. near Agua Caliente in the San Jacinto Mountains, *Parish & Parish 738* (Lectotype: GH; isotypes: PH!, VT!). **Malacothamnus densiflorus* (S. Watson) Greene, Leafl. Bot. Observ. Crit. **1:** 208. 1906.

M. densiflorum var. *typicum* F. Estes, Bull. S. Calif. Acad. Sci. **24:** 85, 1925. The typical variety, see *M. densiflorum*. **Malacothamnus densiflorus* (S. Wats.) Greene.

M. densiflorum var. *viscidum* (Abrams) Estes, Bull. S. Calif. Acad. Sci. **24:** 85. 1925. Basionym: *Malvastrum viscidum* Abrams, Bull. Torrey Bot. Club **34:** 264. 1907. TYPE: California: San Diego Co. Dry hillsides near El Nido, Harvey's Ranch, *Abrams 3528* (Holotype: NY!; isotypes: DS, F!, GH, PH, US). **Malacothamnus densiflorus* (S. Wats.) Greene var. *viscidus* (Abrams) Kearney, Leafl. W. Bot. **6:** 129. 1951.

M. depressum (Bentham) Svenson. **Malvastrum tomentosum* (L.) S.R. Hill subsp. *tomentosum*. *See text.*

M. digitatum Greene, Leafl. Bot. Observ. Crit. **1:** 154. 1905. TYPE: New Mexico: Sierra Co. Kingston, alt. 6600 ft., *Metcalfe 9947* (Holotype: US!; isotypes: CAS, F!, G!, UC!, US!). **Sphaeralcea digitata* (Greene) Rydberg, Bull. Torrey Bot. Club **40:** 58. 1913.

M. diminutivum (Philippi) E. G. Baker, J. Bot. **32:** 36. 1894. Basionym: *Malva diminutiva* Philippi, Anales Mus. Nac. Chile Bot. **2:** 8. 1891. TYPE: Chile: Prov. Tarapacá, Paroma, alt. 3800 m, *Philippi 1822* (Holotype: SGO no *41024;* isotype: SGO no *51995*).

Nototriche diminutiva* (Phil.) I. M. Johnston, J. Arnold Arbor. **19: 260. 1938.

M. dimorphum J. T. Howell. **Malvastrum tomentosum* (L.) S. R. Hill subsp. *tomentosum. See text.*

M. dissectum Harvey in Harvey & Sonder, Fl. Cap. **1:** 164. 1860, non Cockerell, 1900. TYPE: South Africa: Cape Province. Swellendam District, sandy hills near Kochmann's Kloof, *Ecklon & Zeyher 295* (Holotype: s). **Anisodontea dissecta* (Harvey) Bates, Gentes Herb. **10:** 338. 1969.

M. dissectum (Nutt. in Torr. & Gray) Cockerell, Bull. Torrey Bot. Club **27:** 87. 1900, non Harvey in Harvey & Sonder, 1860. Nom. illegit. Basionym: *Sida dissecta* Nuttall in Torr. & Gray, Fl. N. Amer. **1:** 235. 1838. See *M. coccineum* var. *dissectum* above. **Sphaeralcea coccinea* (Nutt.) Rydberg var. *coccinea.*

M. dissectum var. *cockerellii* (A. Nelson) A. Nelson in Coulter & Nelson, Man. Bot. Cent. Rocky Mtns. 318. 1909. Basionym: *Malvastrum cockerellii* A. Nelson, see above. **Sphaeralcea coccinea* (Nutt.) Rydb. var. *coccinea.*

M. divaricatum (Andrews) Gray & Harvey in Harvey & Sonder, Fl. Cap. **1:** 163. 1860. Basionym: *Malva divaricata* Andrews, Bot. Repos. 3: t. 182. 1801. TYPE: t. 182, chosen as lectotype by Bates (1969), based upon plants raised at Hammersmith Nursery. **Anisodontea capensis* (L.) Bates, Gentes Herb. **10:** 327. 1969.

M. dryadifolium Solms-Laubach, Bot. Zeitung **65:** 131, t. 2, f. 6. 1907. TYPE: Bolivia: Dep. Chuquisaca. Near Sucre, alt. 4000 m, *Steinmann s.n.* (no examples known, possibly lost). **Acaulimalva dryadifolia* (Solms) Krap., Darwiniana **19:** 19. 1974.

M. dudleyi Eastwood, Leafl. W. Bot. **1:** 218. 1936. TYPE: California: San Luis Obispo Co. Fern Canyon, 2 mi W of Paso Robles, *Dudley s.n.* (Holotype: CAS no *146103*). **Malacothamnus jonesii* (Munz) Kearney, Leafl. W. Bot. **6:** 135. 1951.

M. dusenii Ekman, Ark. Bot. **13:** 5, t. 1, f. 3. 1914. TYPE: Brazil: Est. Paraná, Serrado Mar, Ypiranga, along railway, *Dusén 7084* (Holotype: s!; isotypes: F!, MICH!, MO!, s!). **Monteiroa dusenii* (Ekman) Krap., Biol. Soc. Argent. Bot. **3:** 242. 1951.

M. elatum (E. G. Baker) A. Nelson, Bot. Gaz. (Crawfordsville) **34:** 25. 1902. Basionym: *Malvastrum coccineum* var. *elatum* E. G. Baker, see above. **Sphaeralcea coccinea* (Nutt.) Rydb. var. *elata* (E. G. Baker) Kearney in Kearney & Peebles.

M. englerianum E. Ulbrich, Bot. Jahrb. Syst. **42:** 115. 1909. TYPE: Peru: Dep. Ancash, Prov. Cajatambo between Tallenga and Piscapaccha, alt., 3800-4000 m, *Weberbauer 2888* (Holotype: B (lost)—photo Field Mus. ser. no. *9312*—F!, fragment of holotype—K!; isotype: MOL). **Acaulimalva engleriana* (Ulbr.) Krap., Darwiniana **19:** 19. 1974.

M. erodifolium (Presl) E. G. Baker, J. Bot. **28:** 369. 1890. Basionym: *Malva erodiifolia* Presl, Reliq. Haenk. **2:** 122. 1835. TYPE: Chile: *Haenke* (Holotype: presumably PR, not seen). This is not *Malvastrum* (corolla purple). The description rather closely resembles that of *Tarasa humile* (Gillies ex Hook & Arn.) Krap., Bol. Soc. Argent. Bot. **5:** 117. 1954.

M. exhumatum Cockerell, Bull. Torrey Bot. Club **33:** 311, f. 5. 1906. TYPE: fossil specimen — Colorado: S W of Florissant, (Oligocene), *Henderson & Ramaley* (Holotype: NY). The illustration shows the leaf of a *Sphaeralcea.* ***Sphaeralcea exhumatum** (Cockerell) S. R. Hill, *comb. nov.*

M. exile A. Gray in Ives, Rep. Colorado River Bot.: **8.** 1861. TYPE: S W United States: Colorado River, sandy areas, Pyramid Canyon, *Newberry s.n.* (Holotype: GH!; isotype: US!). **Eremalche exilis* (A. Gray) Greene, Leafl. Bot. Observ. Crit. **1:** 208. 1906.

M. famatinense Hieronymus ex A. W. Hill, Bot. Jahrb. Syst. **37:** 581, 1906, pro syn. **Nototriche famatinense* A. W. Hill, Bot. Jahrb. Syst. **37:** 581. 1906.

M. fasciculatum (Nuttall ex Torrey & Gray) Greene, Fl. Franciscana: 108. 1891. Basionym: *Malva fasciculata* Nuttall in Torrey & Gray, Fl. N. Am. 1: 225. 1838. TYPE: California: "Santa Barbara", possibly San Diego Co. instead, *Nuttall s.n.* (Holotype: NY; isotypes: GH, PH!). **Malacothamnus fasiciculatus* (Nutt. ex Torr. & Gray) Greene var. *fasciculatus,* Leafl. Bot. Observ. Crit. **1:** 208. 1906.

M. fasciculatum var. *catalinense* (Eastwood) McMinn, Man. Calif. Shrubs: 348. 1939. Basionym: *Malvastrum catalinense* Eastwood, see above. **Malacothamnus fasciculatus* (Nutt. ex. Torr. & Gray) Greene subsp. *catalinensis* (Eastw.) R. W. Thorne.

M. fasciculatum var. *laxiflorum* (A. Gray) Munz & I. M. Johnston, Bull. Torrey Bot. Club **51:** 296. 1924. Basionym: *Malvastrum thurberi* var. *laxiflorum* A. Gray, Proc. Amer. Acad. Arts **22:** 291, in adn. 1887. This name based upon *Malvastrum splendi-*

dum Kellogg, Proc. Calif. Acad. Sci. **1:** 65. 1855. TYPE: *Wallace s.n.*, not preserved. Neotype: California: Los Angeles Co. Santa Monica Mtns., Mulholland Hwy 0.4 mi E of Malibu Lake, *Bates 2493* (Neotype: LA no. *47326*). **Malacothamnus fasciculatus* (Nutt. ex Torr. & Gray) Greene var. *laxiflorus* (A. Gray) Kearney, Leafl. W. Bot. **6:** 137. 1951.

M. fasciculatum var. *nesioticum* (Robins.) McMinn, Man. Calif. Shrubs: 348, f. 396. 1939. Basionym: *Malvastrum nesioticum* Robinson in A. Gray, Syn. Fl. Amer. **1,** 1: 312. 1897. TYPE: California: Santa Barbara Co. Island of Santa Cruz, *Greene s.n.* (Lectotype: GH; isotypes: CAS, ND). **Malacothamnus fasciculatus* (Nutt. ex Torr. & Gray) Greene var. *nesioticus* (Robins.) Kearney, Leafl. W. Bot. **6:** 139. 1951.

M. fasciculatum var. *nuttallii* (Abrams) McMinn, Man. Calif. Shrubs: 348, f. 397, 1939. Basionym: *Malacothamnus nuttallii* Abrams, Bull. New York Bot. Gard. **6:** 417. 1910. TYPE: California: Ventura Co. Casitas Pass, *Abrams s.n.* (Holotype: DS no. *31553;* isotypes: DS, GH). **Malacothamnus fasciculatus* (Nutt. ex Torr. & Gray) Greene var. *nuttallii* (Abrams) Kearney, Leafl. W. Bot. **6:** 138. 1951.

M. fasciculatum var. *typicum* Estes, Bull. S. Calif. Acad. Sci. **24:** 83. 1925. The typical variety, see *M. fasciculatum* above. **Malacothamnus fasciculatus* (Nutt. ex Torr. & Gray) Greene var. *fasciculatus.*

M. fiebrigii Ulbrich, Bot. Jahrb. Syst. **42:** 113. 1909. TYPE: Bolivia: southern region near Puna Patanca, marshy places, alt. 3800 m, *Fiebrig 2963* (Holotype: B (lost) — photo Field Mus. ser. no. *9313* — F!; isotypes: G, K, M). **Acaulimalva nubigena* (Walp.) Krap., Darwiniana **19:** 22. 1974.

M. flabellatum Weddell, Chlor. And. **2:** 281. 1861. TYPE: Bolivia: Dep. La Paz. Summit of the Cordillera of La Paz, *D'Orbigny 332* (Lectotype: P). **Nototriche flabellata* (Wedd.) A. W. Hill, Bot. Jahrb. Syst. **37:** 579. 1906.

M. foliosum S. Watson, Proc. Amer. Acad. Arts **20:** 356. 1885. TYPE: Mexico: Baja California, Santo Tomás, near the coast, *Orcutt s.n.* (Holotype: GH; isotypes: PENN!, PH!, UC, US!). **Malacothamnus foliosus* (S. Wats.) Kearney,, Leafl. W. Bot. **6:** 122. 1951.

M. fragrans (Jacquin) Gray & Harvey in Harvey & Sonder, Fl. Cap. **1:** 159. 1860, non Eastwood, 1936. Basionym: *Malva fragrans*

Jacquin, Horti. Bot. Vindob. **3:** 20, t. 33. 1776. TYPE: t. 33 chosen as lectotype by Bates (1969). **Anisodontea scabrosa* (L.) Bates, Gentes Herb. **10:** 368. 1969.

M. fragrans Eastwood, Leafl. W. Bot. **1:** 218. 1936, non Gray & Harvey in Harvey & Sonder, 1860. TYPE: California: San Luis Obispo Co. El Dorado School near Santa Margarita, *Wall s.n.* (Holotype: CAS no. *204656;* isotypes: GH, US!). **Malacothamnus niveus* (Eastw.) Kearney, Leafl. W. Bot. **6:** 123. 1951.

M. fremontii Torrey ex Gray, Mem. Amer. Acad. Arts n.s. **4:**21, in adn. 1849. TYPE: California: interior, *Fremont s.n.* (Holotype: NY; isotypes: GH, MO!). **Malacothamnus fremontii* (Torr. ex Gray) Greene, Leaf. Bot. Observ. Crit. **1:** 208. 1906.

M. fremontii var. *cercophorum* Robinson in Gray, Syn. Fl. N. Am. **1,** 1: 311. 1897. TYPE: California: Alameda Co., Arroyo del Valle, *Greene s.n.* (Holotype: UC no. *18795;* isotype: GH). **Malacothamnus fremontii* (Torr. ex Gray) Greene subsp. *cercophorus* (Robins.) Munz, Aliso **4:** 94. 1958. ("*cercophorum*").

M. fremontii subsp. *exfibulosum* (Jepson) Wiggins ex Abrams, Illustr. Fl. Pacif. St. **3:** 95. 1951. Basionym: *Sphaeralcea fremontii* (Torr. ex Gray) Jepson var. *exfibulosus* Jepson, Fl. Calif. **2:** 500. 1936. TYPE: California: Yolo Co. Putah Creek, near Winters, gravel bed. *Jepson 16741* (Holotype: JEPS no. *2869*). **Malacothamnus helleri* (Eastw.) Kearney, Leafl. W. Bot. **6:** 124. 1951.

M. fremontii var. *helleri* (Eastwood) McMinn, Man. Calif. Shrubs: 341, f. 388. 1939. Basionym: *Malvastrum helleri* Eastwood, Leafl. W. Bot. **1:** 217. 1936. TYPE: California: Colusa Co. Near Ladoga, *Heller 13242* (Holotype: CAS no. *52632;* isotypes: DS, F!, MO, NY, PENN!, PH!, US, WIS!). **Malacothamnus helleri* (Eastw.) Kearney, W. Bot. **6:** 124. 1951.

M. fremontii var. *niveum* (Eastwood) McMinn, Man. Calif. Shrubs: 343, f. 389. 1939. Basionym: *Malvastrum niveum* Eastwood, Leafl. W. Bot. **1:** 232. 1936. Based upon *Malvastrum fragrans* Eastwood, see above. **Malacothamnus niveus* (Eastwood) Kearney, Leafl. W. Bot. **6:** 123. 1951.

M. fremontii var. *orbiculatum* (Greene) I. M. Johnston, Pl. World **22:** 109. 1919. Basionym: *Malvastrum orbiculatum* Greene, Fl. Francisc.: 109, 1891. TYPE: California; Kern Co. Mountains S of Tehachapi, *Greene s.n.* (Holotype: ND no. *39083*). **Malaco-*

thamnus orbiculatus (Greene) Greene, Leafl. Bot. Observ. Crit. **1:** 208. 1906.

M. gabrielense Munz & I. M. Johnston, Bull. Torrey Bot. Club **52:** 223. 1925. TYPE: California: Los Angeles Co. Arraster, north slope of San Gabriel Mountains, alt. 3100 ft., *Peirson 774* (Holotype: POM no. *9927;* isotypes: JEPS, POM, RSA). **Malacothamnus marrubioides* (Dur. & Hilger) Greene, Leafl. Bot. Observ. Crit. **1:** 208. 1906.

M. garckeanum K. Schumann in Martius, Fl. Bras. **12,** 3: 267, t. 52. f. 1. 1891. TYPE: Uruguay: wet sandy places near Montevideo, *Arechavaleta 288* (Holotype: presumably MVM). **Monteiroa glomerata* (Hook. & Arn.) Krap., Bol. Soc. Argent. Bot. **3:** 239. 1951.

M. garckeanum var. *paranese* K. Schumann in Martius, Fl. Bras. **12,** 3: 267, t. 52, f. 1. 1891 ("*paranensis*"). TYPE: Brazil: Paraná River, *Tweedie s.n.* (No extant specimens known). **Monteiroa glomerata* (Hook. & Arn.) Krap., Bol. Soc. Argent. Bot. **3:** 239. 1951.

M. geranioides (Schlecht. & Cham.) Hemsley, Biol. Centr. Am. Bot. **1:** 99. 1879. Basionym: *Malva geranioides* Schlechtendal & Chamisso, Linnaea **5:** 226. 1830, non Gillies ex Hook. & Arn., 1833. TYPE: Mexico: Veracruz. Llanos de Perote, *Schiede & Deppe 577* (Holotype: HAL no. *43666;* isotype: B (lost) — photo Field Mus. ser. no. *18272* at F!). **Tarasa geranioides* (Schlecht. & Cham.) Krap., Bol. Soc. Argent. Bot. **5:** 125. 1954.

M. geranioides var. *galanderi* (O. Kuntze) Seckt, Fl. Cord: 346. 1930. Basionym: *Malveopsis geranioides* (Schlecht. & Cham.) O. Ktze. var. *galanderi* O. Kuntze, Rev. Gen. **3,** 2: 21. 1898. TYPE: Argentina: Prov. Córdoba. Cañada del Molina, *Galander s.n.* (Holotype: NY!). **Tarasa antofagastana* (Phil.) Krap., Bol. Soc. Argent. Bot. **5:** 130. 1954.

M. geranioides var. *subsessile* (O. Kuntze) Seckt, Fl. Cord.: 346. 1930. Basionym: *Malveopsis geranioides* (Schlecht. & Cham.) O. Kuntze var. *subsessilis* O. Kuntze, Rev. Gen. **3,** 2: 21. 1898. TYPE: Argentina: Prov. Córdoba, Sierra Córdoba, *Kurtz s.n.* (Holotype: NY!). **Tarasa antofagastana* (Phil.) Krap., Bol. Soc. Argent. Bot. **5:** 130. 1954.

M. gilliesii (Steud.) J. G. Baker, Gard, Chron. **24:** 166. 1885. Basionym: *Malva gilliesii* Stüdel, Nom. Bot. **2:** 94. 1841, non Phi-

lippi, 1870. Based upon: *Malva geranioides* Gillies ex Hooker & Arnott, Bot. Misc. **3:** 152. 1833, non Schlecht. & Cham., 1830. Nom. illegit. TYPE: Argentina: Mendoza, *Gillies s.n.* (Disposition of types not known, duplicate OXF!). **Modiolastrum gilliesii* (Steud.) Krap., Lilloa **19:** 123, in adn. 1949.

M. glomeratum (Hooker & Arnott) Grisebach, Abh. Königl. Ges. Wiss. Göttingen **24:** 42. 1879. Basionym: *Malva glomerata* Hooker & Arnott, Bot. Misc. **3:** 151. 1833. TYPE: Argentina: woods of the Paraná, Buenos Aires, *Tweedie 1037* (Holotype: K; Prob. isotype: OXF!). **Monteiroa glomerata* (Hook. & Arn.) Krap., Bol. Soc. Argent. Bot. **3:** 239. 1951.

M. gracile Eastwood, Leafl. W. Bot. **1:** 219. 1936. TYPE: California: San Luis Obispo Co. Road between Arroyo Grande and Huasna, *Eastwood 14996* (Holotype: CAS; isotypes: CAS, DS, F! GH, POM, RSA, US!). **Malacothamnus gracilis* (Eastw.) Kearney, Leafl. West. Bot. **6:** 130. 1951.

**M. grandiflorum* Krapovickas. *See text.*

M. greemanianum Rose, Contr. U. S. Natl. Herb. **5:** 180. 1897. TYPE: Mexico: Federal District, Valley of Mexico near Contreras at Eslava, *Pringle 6582* (Holotype: US no. *316693!;* isotypes: BKL! BM, F! G, GH! K, MO! ND, NY! PH! UC, VT!). **Kearnemalvastrum subtriflorum* (Lag.) Bates, Brittonia **19:** 232. 1967.

M. grossulariifolium (Hook. & Arn.) A. Gray, Mem. Amer. Acad. Arts n.s. **4:**21, in adn. 1849 ("*grossulariaefolium*"). Basionym: *Sida grossulariifolia* Hooker & Arnott, Bot. Beechey Voy.: 326. 1838 ("*grossulariaefolia*"). See *M. coccineum* var. *grossulariifolium* above. **Sphaeralcea grossulariifolia* (Hook. & Arn.) Rydberg.

M. grosulariifolium (Cavanilles) Gray & Harvey in Harvey & Sonder, Fl. Cap. **1:** 161. 1860 ("*grossulariaefolium*") quoad basionym, non Gray, 1849. Basionym: *Malva grosulariifolia* Cavanilles, Diss. **2:** 71, t. 24, f. 2. 1786. ("*grosulariaefolia*"). TYPE: The lectotype chosen by Bates (1969) is t. 169, f. 207 in Dillenius, Hort. Eltham. **2:** 209. 1732. **Anisodontea scabrosa* (L.) Bates, Gentes Herb. **10:** 368. 1969.

M. grosulariifolium sensu Garcke, Bot. Zeitung **22:** 11. 1864, ("*grossularifolium*"), excl. basionym, non Gray, 1849 nec Gray & Harvey, 1860. **Anisodontea biflora* (Desr.) Bates, Gentes Herb. **10:** 340. 1969.

M. grosulariifolium sensu A. Gray & Harvey in Harvey & Sonder, Fl. Cap. **1:** 161. 1860 ("*grossulariaefolium*"), excl. basionym. **Anisodontea triloba* (Thunb.) Bates, Gentes Herb. **10:** 363. 1969.

M. grosulariifolium var. *β parvifolium* Harvey in Harvey & Sonder, Fl. Cap. **1:** 161. 1860, excl. specim. *Drège 7322*. TYPE: South Africa: Cape Province, Beaufort West District, Nieuweveldsbergen near Beaufort, alt. 3000 5000 ft., *Drège s.n.* (Lectotype: s; isotypes: G! K, L, MO, P). **Anisodontea triloba* (Thunb.) Bates, Gentes Herb. **10:** 363. 1969.

M. guaraniticum Hassler. **Malvastrum tomentosum* (L.) S. R. Hill. *See text.*

**M. guatemalense* Standley & Steyermark. *See text.*

M. hallii Eastwood, Leafl. W. Bot. **1:** 216, 1936. TYPE: California: Contra Costa Co., west side of Pine Canyon, Mt. Diablo, *Hall & Essig 10131* (Holotype: CAS no. *143419;* isotypes: DS, F! LA, MO! NY! POM, UC, US!, WIS!) **Malacothamnus hallii* (Eastw.) Kearney, Leafl. W. Bot. **6:** 134. 1951.

M. hauthalii Ulbrich, Bot. Jahrb. Syst. **42:** 114. 1909. TYPE: Bolivia: Dep. La Paz. Between Palca and Illimani, alt. 4000 4800 m, *Hauthal 311* and *347* (Fragment of type specimens at K! but unnumbered; Photo of *Hauthal 347 (*B) available at Field Mus. ser. no. *9315*—F!). **Acaulimalva dryadifolia* (Solms) Krap., Darwiniana **19:** 19. 1974.

M. helleri Eastwood, Leafl. W. Bot. **1:** 217. 1936. **Malacothamnus helleri* (Eastw.) Kearney. See *M. fremontii* var. *helleri.*

M. heterophyllum Grisebach, Abh. Königl. Ges. Wiss. Göttingen **24:** 43. 1879. TYPE: Bolivia: Tarija, *Lorentz & Hieronymus 971* (Lectotype: GOET!; isotypes: CORD,, SI, UC). **Tarasa heterophylla* (Griseb.) Krap., Bol. Soc. Argent, Bot. **5:** 124. 1954.

M. hinkleyorum I. M. Johnston, Contr. Gray Herb. n.s. **70:** 73. 1924. TYPE: Peru: Dep. Arequipa. South slope of Chachani Mt., near Arequipa, *Hinkley & Hinkley 43* (Holotype: GH; isotype: US!) **Urocarpidium chilense* (Braun & Bouchè) Krap., Darwiniana **10:** 619. 1954.

M. hirtipes Spegazzini, Physis (Buenos Aires) **3:** 168. 1917. TYPE: Argentina: Prov. Salta. Nevado de Cachi, alpine meadows, alt. 4000 m, *Spegazzini 20001* (Holotype: LP). **Nototriche hirtipes* (Spegazzini) B. L. Burtt & A. W. Hill, Kew Bull.: 130. 1948.

This may be a synonym of *Nototriche anthemidifolia* (Remy) A. W. Hill (see Krapovickas, 1957).

**M. hispidum* (Pursh) Hochreutiner. *See text.*

M. hornschuchianum (Walpers) Macbride, Publ. Field Mus. Nat. Hist., Bot. Ser. **13, 3a:** 519. 1956. Basionym: *Malva hornschuchiana* Walpers, Nov. Actorum Acad. Caes. Leop. – Carol. Nat. Cur. 19, suppl. **1:** 303. 1843. TYPE: Peru: Dep. Arequipa, Arequipa, *Meyen s.n.* (Holotype: B (lost) — photo Field Mus. ser. no. *9332*). **Tarasa hornschuchiana* (Walp.) Krap., Bol. Soc. Arg. Bot. **5:** 139. 1954. Considered a synonym of *T. capitata* (Cav.) Bates by Bates, Gentes Herb. **9:** 388. 1965.

M. howellii Eastwood, Leafl. W. Bot. **1:** 220. 1936. TYPE: California: Contra Costa Co. Nortonville,, *Howell 6470* (Holotype: CAS no. *204366;* isotypes: F! GH, MO, POM, US!). **Malacothamnus howellii* (Eastw.) Kearney, Leafl. W. Bot. **6:** 126. 1951.

M. howellii var. *cordatum* Eastwood, Leafl. W. Bot. **2:** 220. 1936. TYPE: California: Stanislaus Co. Junto del Puerto Canyon, *Dudley s.n.* (Holotype: CAS no. *227909;* isotypes: DS, GH, NY, POM). **Malacothamnus howellii* (Eastw.) Kearney, Leafl. W. Bot. **6:** 126. 1951.

M. humile (Gillies ex Hooker & Arnott) A. Gray, Bot. U. St. Expl. Exped. **1:** 150, in adn. 1854. Basionym: *Malva humilis* Gillies ex Hooker & Arnott, Bot. Misc. **3:** 150. 1833. TYPE: Argentina: Prov. Mendoza. Andes of Mendoza, El Valle Hermoso, *Gillies s.n.* (Holotype: K; isotypes: GH! GL, OXF! SGO). **Tarasa humilis* (Gillies ex Hook. & Arn.) Krap., Bol. Soc. Argent. Bot. **5:** 117. 1954.

M. humile var. *subacaule* (Philippi) Reiche, Anales Univ. Chile **91:** 382. 1895. Basionym: *Malva subacaulis* Philippi, Anales Univ. Chile **82:** 14. 1893, non Coss ex E. G. Baker, 1890. TYPE: Chile: Prov. Curicó, hot springs at Peteroa, *Vidal 2332* (Holotype: SGO no. *52006;* isotype: SGO no. *41013*). **Tarasa humilis* (Gillies ex Hook. & Arn.) Krap., Bol. Soc. Argent. Bot. **5:** 117. 1954.

M. hypomadarum Sprague, Gard. Chron. **43:** 394, in adn., f. 176. 1908. TYPE: Cultivated material from the nursery of Veitch & Sons (Holotype: K; isotype: K!). **Anisodontea*×*hypomadarum* (Sprague) Bates, Gentes Herb. **10:** 250. 1969. ("*hypomandarum*").

M. incanum (Godron) Thellung, Mém. Soc. Sci. Nat. Cherbourg ser. **4,** 38: 377. 1912. Basionym: *Malva incana* Godron, Mém.

Sect. Sci. Acad. Sci. Montpellier **1:** 419. 1853, non Presl, 1835. TYPE: France: an adventive at Port-Juvénal, 15 October 1852, *Touchy s.n.* (Holotype: MPU!). Thellung's discussion and citation of *Fiebrig 3083* as a representative specimen led Krapovickas (1957) to interpret this as: **Sphaeralcea bonariensis* (Cav.) Griseb., Abh, Königl, Ges. Wiss. Göttingen **19:** 92. 1874.

M. insulare Kearney, Leafl. W. Bot. **6:** 167. 1952. TYPE: Ecuador: Galápagos Islands. Albemarle (Isabella) Island, summit of Tagus Cove Mountain, *Howell 9570* (Holotype: CAS no. *362992*). **Urocarpidium insulare* (Kearney) Krap., Darwiniana **10:** 631. 1954.

**M. interruptum* K. Schumann in Martius. *See text.*

M. involucratum Robinson in A. Gray, Syn. Fl. N. Am. **1,** 1: 310. 1897. TYPE: California: Monterey Co., at Jolon, *Brandegee s.n.* (Lectotype: GH). **Malacothamnus palmeri* (S. Wats.) Greene var. *involucratus* (Robins.) Kearney, Leafl. W. Bot. **6:** 121. 1951.

M. jacens S. Watson, Proc. Amer. Acad. Arts **21:** 417. 1886. TYPE: Mexico: Est. Chihuahua, Norogachi, 150 mi N of Batopilas, *Palmer 430* (Lectotype: GH!; isotypes: K, US!). **Urocarpidium jacens* (S. Wats.) Krap., Darwiniana **10:** 627. 1954.

M. jacens var. *genuinum* Hochreutiner, Annuaire Conserv. Jard. Bot. Genève **6:** 32. 1902. The typical variety, see *M. jacens.* **Urocarpidium jacens* (S. Wats.) Krap.

M. jacens var. *palmatifidum* Hochreutiner, Annuaire Conserv. Jard. Bot. Genève **6:** 32. 1902. TYPE: Mexico: Est. Chihuahua, Sierra Madre, *Pringle 1574* (Holotype: G!; isotypes: BM! BR! G! UC). **Urocarpidium palmatifidum* (Hochr.) Krap., Darwiniana **10:** 623. 1954.

M. jonesii Munz, Bull. S. Calif. Acad. Sci. **24:** 88. 1925. TYPE: California: San Luis Obispo Co. Paso Robles, *Jones 223* (Holotype: POM no. *60429*). **Malacothamnus jonesii* (Munz) Kearney, Leafl. W. Bot. **6:** 135. 1951.

M. jorgensenii I. M. Johnston, Contr. Gray Herb. n.s. **70:** 76. 1924. TYPE: Argentina: Prov. Tucumán. Near Suncho. *Jörgensen 1389* (Holotype: GH! isotype: MO). **Tarasa jorgensenii* (I. M. Johnst.) Krap., Bol. Soc. Argent. Bot. **5:** 138. 1954. According to Bates (1965) this is a synonym of *Tarasa capitata* (Cav.) Bates, Gentes Herb. **9:** 388. 1965.

M. kernense (C. B. Wolf) Munz, Aliso **4:** 93. 1958. Basionym: **Eremalche kernensis* C. B. Wolf, Occas. Pap. Ranch. Santa Ana Bot. Gard. **1:** 66, f. 18. 1938. TYPE: California: Kern Co. Temblor Valley, 7 mi NW of McKittrick on Lost Hills Rd., alt. 900 ft., *Wolf 8413* (Holotype: RSA; isotypes: CAS, US!). Closely allied and perhaps conspecific with *E. exilis* (A. Gray) Greene.

M. lacteum (Aiton) Garcke in Braun & Bouché, Index Sem. Hort. Bot. Berol.: 17. 1866. Basionym: *Malva lactea* Aiton, Hort. Kew. **2:** 448. 1789. TYPE: Cultivated plant introduced in 1780 by B. Bewick, grown in 1781 at the Royal Botanic Gardens, Kew (Holotype: BM — photos BH neg. no. *15163* and US neg. no. *635*). **Kearnemalvastrum lacteum* (Ait.) Bates, Brittonia **19:** 231. 1967.

M. lasiocarpum (St.-Hilaire & Naudin) Grisebach, Abh. Königl. Ges. Göttingen **24:** 43. 1879. Basionym: *Malva lasiocarpa* St.-Hilaire & Naudin, Ann. Sci. Nat. Bot. ser. 2, **18:** 45. 1842. TYPE: Brazil: Rio Grande do Sul, probably collected by *Sellow* (Holotype: presumably RB; isotype: P). **Modiolastrum lateritium* (Hooker) Krap., Revista Argent. Agron. **12:** 39. 1945. Cited as a synonym by Krapovickas (1957).

M. lateritium (Hooker) Nicholson, Illust. Dict. Gard. **2:** 319. 1885. Basionym: *Malva lateritia* Hooker, Bot. Mag. **14:** t. 3846. 1841. TYPE: Argentina: Buenos Aires, *Tweedie s.n.* (Holotype: no specimens at K; probable isotype OXF! from Rio de la Plata); **Modiolastrum lateritium* (Hooker) Krap., Revista Argent. Agron. **12:** 39. 1945.

M. laxiflorum (A. Gray) ex Davidson & Moxley, Fl. S. Calif.: 233. 1923, new combinations not indicated. Basionym: *Malvastrum thurberi* var. *laxiflorum* A. Gray, Proc. Amer. Acad. Arts **22:** 291, in adn. 1887. See *M. fasciculatum* var. *laxiflorum* above. **Malacothamnus fasciculatus* (Nutt. ex Torr. & Gray) Greene var. *laxiflorus* (A. Gray) Kearney.

M. leptophyllum A. Gray, Pl. Wright. **1:** 17. 1852. TYPE: Texas: Between W. Texas and El Paso. New Mexico, *Wright s.n.* (Holotype: GH). **Sphaeralcea leptophylla* (A. Gray) Rydberg, Bull. Torrey Bot. Club. **40:** 59. 1913.

M. limense (Linnaeus) J. Ball, J. Linn. Soc. Bot. **22:** 32. 1885. Basionym: *Malva limensis* Linnaeus, Cent. Pl. **2:** 27. 1756. TYPE: America, specimen from *Miller* (Holotype: LINN micro-

fiche no. 870.6). **Urocarpidium limense* (L.) Krap., Kurtziana **4:** 33. 1967.

M. lindheimerianum (Scheele) Walpers. **Malvastrum coromandelianum* (L.) Garcke. *See text.*

M. linearifolium Buckley, Proc. Acad. Nat. Sci. Philadelphia **13:** 449. 1861. TYPE: Northern Texas. *Buckley* (Holotype: PH!). **Sida ciliaris* L. var. *fasciculata* (Torr. & Gray) A. Gray, Proc. Amer. Acad. Arts **22:** 294. 1886.

M. linoide Hieronymus, Bol. Acad. Nac. Ci. **3:** 336. 1879. TYPE: Argentina: northern bank of Río Negro, hills, far below Carmen de Patagones, *Berg 85* (Holotype: CORD). **Lecanophora ecristata* (A. Gray) Krap., Darwiniana **9:** 264. 1950.

M. lobbii E. G. Baker, J. Bot. **29:** 365. 1891. TYPE: Colombia? *Lobb* (Holotype: K). **Nototriche lobbii* (E. G. Baker) A. W. Hill, Bot. Jahrb. Syst. **37:** 579. 1906.

M. lobulatum Weddell ex Mandon, Bull. Soc. France **12:** 82. 1865. Nomen nudum, new comb. not indicated. Presumed basionym: *Malva parnassiifolia* (Hk.) Weddell var. *β lobulata* Weddell, Chlor. And. **2:** 276. 1861. TYPE: Bolivia: Dep. Chuquisaca: between río Pilcomayo and the town of Camargo, *Weddell 3931* (Holotype: P). The specimen cited by Mandon, *Mandon 799,* is the type of *Malvastrum obcuneatum* E. G. Baker. **Acaulimalva nubigena* (Walp.) Krap., Darwiniana **19:** 22. 1974.

M. longirostre Weddell, Chlor. And. **2:** 281. 1861. TYPE: Peru: Dep. Cuzco, Andes of Cuzco, *Castelnau s.n.* (Holotype: P). **Nototriche longirostris* (Wedd.) A. W. Hill, Bot. Jahrb. Syst. **37:** 579. 1906.

M. macleanii A. Gray, Bot. U. St. Expl. Exped. **1:** 152, in adn. 1854 ("*macleani*"). TYPE: Peru: High Andes, *Maclean s.n.* (Holotype: K). **Nototriche macleanii* (A. Gray) A. W. Hill, Bot. Jahrb. Syst. **37:** 579. 1906.

M. macrostachyum (Presl) Hemsley. **Malvastrum americanum* (L.) Torrey in Emory. *See text.*

M. mandonianum Weddell, Chlor. And. **2:** 282. 1861. TYPE: Bolivia: Cordillera of Sorata, *Mandon s.n.* (Lectotype: P). **Nototriche mandoniana* (Wedd.) A. W. Hill, Bot. Jahrb. Syst. **37:** 579. 1906.

M. mandonii (E. G. Baker) Macbride, Publ. Field Mus. Nat. Hist., Bot. Ser. **13, 3a:** 520. 1956 ("*mandoni*"). Basionym: *Sphaeral-*

cea mandonii E. G. Baker, J. Bot. **31:** 364. 1893. ("*mandoni*"). TYPE: Bolivia: Dep. La Paz, Prov. Larecaja, near Sorata in woodlands, alt. 2800 3000 m, *Mandon 808* (Holotype: K; isotypes: BM, G, NY!). **Tarasa mandonii* (E. G. Baker) Kearney, Leafl. W. Bot. **5:** 190. 1949.

M. marrubioides Durand & Hilger, J. Acad. Nat. Sci. Philadelphia ser. 2, **3:** 38. 1855. TYPE: California, Madera or Fresno Co. Fort Miller (Millerton), *Heermann s.n.* (Holotype: P; isotypes: GH, PH!, US!). **Malacothamnus marrubioides* (Dur. & Hilg.) Greene, Leafl. Bot. Observ. Crit. **1:** 208. 1906.

M. marrubioides var. *paniculatum* A. Gray, Proc. Amer. Acad. Arts **22:** 290, in adn. 1887. TYPE: Mexico: Baja California. Ensenada de Todos Santos, *Orcutt s.n.* (Holotype: GH; isotypes: UC, US!). **Malacothamnus paniculatus* (A. Gray) Kearney, Leafl. W. Bot. **6:** 123. 1951.

M. marrubioides var. *viscidum* (Abrams) McMinn, Man. Calif. Shrubs: 345. 1939. Basionym: *Malvastrum viscidum* Abrams. See *M. densiflorum* var. *viscidum* above. **Malacothamnus densiflorus* (S. Wats.) Greene var. *viscidus* (Abrams) Kearney.

M. megalorrhizum (Philippi) E. G. Baker, J. Bot. **29:** 363. 1891. Basionym: *Sida megalorrhiza* Philippi, Fl. Atac.: 11. 1860. TYPE: Chile: Atacama, Alto de Paquios, 23° 50′ lat., alt. 12600 ft., *Philippi s.n.* (Holotype: SGO no. *51954*; isotype: K). **Nototriche megalorrhiza* (Phil.) A. W. Hill, Bot. Jahrb. Syst. **37:** 579. 1906.

M. mendocinense Eastwood, Leafl. W. Bot. **2:** 188. 1939. TYPE: California: Mendocino Co. 5 mi. from Ukiah towards Booneville, *Eastwood & Howell 4582* (Lectotype: CAS no. *249530*), **Malacothamnus mendocinensis* (Eastw.) Kearney, Leafl. W. Bot. **6:** 133. 1951.

M. meridae A. W. Hill, J. Linn. Soc. Bot. **39:** 226. 1909. TYPE: Venezuela: Prov. Merida, Páramo de Mucuchies, alt. 3900 m, *Linden 1425* (Lectotype: K; isotypes: BM, OXF! P). **Acaulimalva purdiaei* (A. Gray) Krap., Darwiniana **19:** 26. 1974. See *M. acaule* var. *granatense*.

M. mexicanum (Schauer) Hemsley, Biol. Centr. Am. Bot. **1:** 99. 1879. Basionym: *Malva mexicana* S. Schauer, Linnaea **20:** 724. 1847. non Sessé & Mociño, 1889. TYPE: Mexico: Est. Hidalgo. Near Zimapan, *Aschenborn 614* (Holotype: B (lost)—photo

Field Mus. neg. *18273*). **Kearnemalvastrum subtriflorum* (Lag.) Bates, Brittonia **19:** 232. 1967.

1. meyenii Solms ex Ulbrich, Bot. Jahrb. Syst. **42:** 121. 1908, pro syn. **Nototriche meyenii* Ulbrich, Bot. Jahrb. Syst. **42:** 120. 1908.

M. micranthum Wooton & Standley, Contr. U. S. Natl. Herb. **16:** 147. 1913, non Rusby, 1920. TYPE: New Mexico: Tiznitzin, *Wooton 2673* (Holotype: US; isotype: RM). **Sphaeralcea coccinea* (Pursh) Rydberg var. *elata* (E. G. Baker) Kearney, Univ. Calif. Publ. Bot. **19:** 97. 1936.

M. micranthum Rusby, Descr. New Sp. S. Amer. Pl.: 55. 1920, non Woot. & Standl., 1913. nom. illeg. TYPE: Bolivia: Dep. La Paz, La Paz, alt. 3700 m., *Buchtien 2893* (Holotype: NY; isotype: US!). **Tarasa tenella* (Cav.) Krap., Bol. Soc. Argent. Bot. **5:** 123. 1954.

M. modioliforme (O. Kuntze) K. Schumann, Bot. Jahresber. (Just) **26:** 355. 1898. Basionym: *Malveopsis modioliformis* O. Kuntze, Rev. Gen. **3,** 2: 21. 1898. TYPE: Argentina: Prov. Formosa, Colonia Aquino on the Río Paraguay near the mouth of the Río Tebicuari, *Kuntze s.n.* (Holotype: NY; isotypes: B (lost) – photo Field Mus. ser. no. *9328* — F!, US). **Modiolastrum malvifolium* (Griseb.) K. Schumann in Martius, Flor. Bras. 12, **3:** 277. 1891.

M. mollendoense Ulbrich, Bot. Jahrb. Syst. **42:** 120. 1909. TYPE: Peru: Dep. Arequipa, near Mollendo, sandy hill, alt. 100 m, *Weberbauer 1548* (Holotype: B (lost) — photo Field Mus. ser. no. *9319* — F!). **Palaua guntheri* Bruns, Mitt. Inst. Allg. Bot. Hamburg **8:** 56, t. 8, f. 1–2. 1929.

M. multicaule Britton, Bull. Torrey Bot. Club. **16:** 153. 1889. Basionym: *Malva multicaulis* Schlechtendal ex Britton, Bull. Torrey Bot. Club **16:** 153. 1889, pro syn. TYPE: Peru: Asangaro, *Lechler 1784* (Holotype: K). **Tarasa tenella* (Cav.) Krap., Bol. Soc. Argent. Bot. **6:** 123. 1954.

M. multiflorum Greene, Fl. Francisc.: 109. 1891. TYPE: California: Monterey Co.?, collector? *11* (Holotype: UC). **Sphaeralcea coulteri* (S. Wats.) A. Gray, Proc. Amer. Acad. Arts **22:** 291. 1887.

M. munroanum (Douglas ex Lindley) A. Gray, Mem. Amer. Acad. Arts n.s. **4:** 21, in adn., 1849, excl. syn. *Malva fasciculata* Nutt.

in Torr. & Gray. Basionym: *Malva munroana* Douglas ex Lindley, Edward's Bot. Reg. **16:** 1306. 1830. TYPE: Barren plains of the Columbia River, *Douglas s.n.* (Holotype: K; isotype: OXF!) **Sphaeralcea munroana* (Douglas ex Lindl.) Spach in Gray, Proc. Amer. Acad. Arts **22:** 292. 1887.

M. nesioticum Robinson in A. Gray, Syn. Fl. N. Am. 1, **1:** 312. 1897. See *M. fasciculatum* var. *nesioticum* above. **Malacothamnus fasciculatus* (Nutt. ex Torr. & Gray) Greene var. *nesioticus* (Robins.) Kearney.

M. nesioticum subsp. *nuttallii* (Abrams) Wiggins in Abrams, Illus. Fl. Pacif. St. **3:** 94. 1951. See *M. fasciculatum* var. *nuttallii* above. **Malacothamnus fasciculatus* (Nutt. ex Torr. & Gray) Greene var. *nuttallii* (Abrams) Kearney.

M. niveum Eastwood, Leafl. W. Bot. **1:** 232. 1936. Nom. nov. for *Malvastrum fragrans* Eastw., an illegitimate name. See *M. fragrans* above. **Malacothamnus niveus* (Eastw.) Kearney, Leafl. W. Bot. **6:** 123. 1951.

M. nototrichoides Hochreutiner, Candollea **15:** 177. 1956. TYPE: Peru: Dep. Arequipa. Tinopalca, alt. 4200 m., *Rauh & Hirsch P. 628* (Holotype: G!). **Tarasa nototrichoides* (Hochr.) Krap., (pers. comm.) This plant strongly resembles *Tarasa geranioides* (Schlecht. & Cham.) Krap.

M. nubigenum (Walpers) E. G. Baker, J. Bot. **28:** 370. 1890. Basionym: *Sida nubigena* Walpers, Nov. Actorum Acad. Caes. Leop.-Carol. Nat. Cur. 19, Suppl. **1:** 307. 1843. TYPE: Peru: plains around Tissaloman, *Meyen s.n.* (Holotype: B— lost). **Acaulimalva nubigena* (Walp.) Krap., Darwiniana **19:** 22. 1974.

M. nubigenum var. *bipinnatifidum* R. E. Fries, Kongl. Svenska Vetenskapsakad. Handl. ser. 2, **24:** 11, t. 2, f. 10. 1974. TYPE: Bolivia: Dep. La Paz. Prov. Ingavi, Viacha, alt. 3850 m, *Asplund 2118* (Holotype: S). **Acaulimalva nubigena* (Walp.) Krap., Darwiniana **19:** 22. 1974.

M. nudum K. Schumann in Martius, Fl. Bras. 12, **3:** 274. 1891. TYPE: Lectotypification must await further information on disposition of specimens: Uruguay: clay areas near Montevideo, *Arechavaleta 352* (MVM), Argentina: near Buenos Aires, *Tweedie* (B-(lost) — photo Field Mus. ser. no. *9320* — F!, presumably also at W). **Sphaeralcea decipiens* (St.-Hil. & Naud.) Krap., Lilloa **17:** 216. 1949.

M. nuttallii Abrams ex Davidson & Moxley, Fl. S. Calif.: 233. 1923, nomen nudum. New combination not indicated, no reference made to the possible basionym, *Malacothamnus nuttallii* Abrams, Bull. New York Bot. Gard. **6:** 417. 1910. **Malacothamnus fasciculatus* (Nutt. ex Torr. & Gray) Greene var. *nuttallii* (Abrams) Kearney. See *M. fasciculatum* var. *nuttallii.*

M. nuttallii (Abrams) Eastwood, Leafl. W. Bot. **1:** 217. 1936. Basionym: *Malacothamnus nuttallii* Abrams, Bull. New York Bot. Gard. **6:** 417. 1910. See *M. fasciculatum* var. *nuttallii* above. **Malacothamnus fasciculatus* (Nutt. ex Torr. & Gray) Greene var. *nuttallii* (Abrams) Kearney.

M. oaxacanum Rose ex H. B. Davis, Life and Work of C. G. Pringle: 405. 1936, Nom. nud. **Malvastrum bicuspidatum* (S. Watson) Rose subsp. *oaxacanum* S. R. Hill. *See text.*

M. obcuneatum E. G. Baker, J. Bot. **29:** 363. 1891. TYPE: Bolivia: Dep. La Paz, near La Paz. *Mandon 799* (Holotype: BM; isotype: GH). **Nototriche obcuneata* (E. G. Baker) A. W. Hill, Bot. Jahrb. Syst. **37:** 579. 1906.

M. operculatum (Cavanilles) E. G. Baker, J. Bot. **28:** 370. 1890. While published with a '?', this combination is valid in accordance with Art. 34 Note 1. of the International Code of Botanical Nomenclature (Stafleu et al., 1972). The same combination was later made by Hochreutiner, Annuaire Conserv. Jard. Bot. Genève **20:** 129. 1917. *Basionym: Malva operculata* Cavanilles, Diss. **2:** 65, t. 35, f. 1. 1786. TYPE: Peru: sandy places, province of Hoara, *Dombey s.n.* (Holotype: MA; isotype: G!). **Tarasa operculata* (Cav.) Krap., Bol. Soc. Argent. Bot. **5:** 134. 1954.

M. orbiculatum Greene, Fl. Francisc.: 109. 1891. See *M. fremontii* var. *orbiculatum* above. **Malacothamnus orbiculatus* (Greene) Greene.

M. orbignyanum Weddell, Chlor. And. **2:** 279. 1861. TYPE: Bolivia: Dep. Potosi, near Quebrada de las Lagunas, *D'Orbigny 1351* (Holotype: P). **Nototriche orbignyana* (Wedd.) A. W. Hill, Bot. Jahrb. Syst. **37:** 1906.

M. oriastrum (Weddell) E. G. Baker, J. Bot. **28:** 370. 1890. Basionym: *Malva oriastrum* Weddell, Chlor. And. **2:** 277. 1861. TYPE: Bolivia: Dep. Chuquisaca, punas, alt. 3500 m, *Weddell 3962* (Holotype: P, fragment-K). **Acaulimalva oriastrum* (Wedd.) Krap., Darwiniana **19:** 24. 1974.

M. palmeri S. Watson, Proc. Amer. Acad. Arts **12:** 250. 1877. TYPE: California: San Luis Obispo Co. Cambria, *Palmer 50* (Holotype: GH: isotypes: CAS, F!, NY, PH!, UC, US!). **Malacothamnus palmeri* (S. Wats.) Greene, Leafl. Bot. Observ. Crit. **1:** 208. 1906.

M. palmeri var. *involucratum* (Robinson) McMinn, Man. Calif. Shrubs: 339. 1939. Basionym: *Malvastrum involucratum* Robinson in A. Gray, see above. **Malacothamnus palmeri* (S. Wats.) Greene var. *involucratus* (Robins.) Kearney.

M. palustre Ekman, Ark. Bot. **13:** 8, t. 1, f. 2. 1914. TYPE: Brazil. Est. Paraná, high plains at Curytiba, swampy woods, *Dusén 8720* (Lectotype: S!; isotypes: F! MICH!, MO!). **Modiolastrum palustre* (Ekman) Krap., Bol. Soc. Argent. Bot. **7:** 38. 1957.

M. paniculatum (A. Gray) Wiggins, Madroño **10:** 184. 1950. Basionym: *Malvastrum marrubioides* Durand & Hilger var. *paniculatum* A. Gray, see above. **Malacothamnus paniculatus* (A. Gray) Kearney.

M. pappei E. G. Baker, J. Bot. **29:** 166. 1891. TYPE: South Africa: Cape of Good Hope, *Pappe s.n.* (Holotype: K; isotype: TCD). **Anisodontea procumbens* (Harvey) Bates, Gentes Herb. **10:** 331. 1969.

M. parishii Eastwood, Leafl. W. Bot. **1:** 216. 1936. TYPE: California: vicinity of San Bernardino, alt. 300–500 m, *Parish 3804* (Holotype: CAS no. *52756*; isotype: UC). **Malacothamnus parishii* (Eastw.) Kearney, Leafl. W. Bot. **6:** 136. 1951.

M. parnassiifolia (Hooker) A. Gray, Bot. U. St. Expl. Exped. **1:** 150, in adn. 1854. ("*parnassiaefolium*"). Basionym: *Sida parnassiifolia* Hooker, Ic. Pl. ser. 1, **4:** t. 385. 1841. ("*parnassiaefolia*"). TYPE: Ecuador: Prov. Pichincha. Andes of Quito between Guamote and Achupallas, alt. 12000 ft., *Jameson s.n.* (Holotype: K!). **Acaulimalva parnassiifolia* (Hook.) Krap., Darwiniana **19:** 25. 1974 ("*parnassiaefolia*").

M. parnassiifolium var. *lobulatum* (Weddell) E. G. Baker, J. Bot. **29:** 171. 1891. Basionym: *Malva parnassiifolia* (Hk.) Weddell var. *β lobulata* Weddell, Chlor. And. **2:** 276. See *M. lobulatum* above. **Acaulimalva nubigena* (Walp.) Krap.

M. parryi Greene, Fl. Francisc.: 108. 1891. TYPE: California: Tulare Co. Tulare, *Parry s.n.* (Lectotype: ND — Greene Herbarium no. *39088*). **Eremalche parryi* (Greene) Greene, Leafl. Bot. Observ. Crit. **1:** 208. 1906.

M. parviflorum Philippi, Anales Mus. Nac. Chile Bot. **2:** 9. 1891. TYPE: Chile: Prov. Atacama. Alto de Machuca, *Philippi 1855* (Lectotype: SGO no. *41050*; isotype: K, SGO no. *51992*). **Nototriche parviflora* (Phil.) A. W. Hill, Bot. Jahrb. Syst. **37:** 579. 1906.

M. pearcei E. G. Baker, J. Bot. **29:** 364. 1891. TYPE: Peru: Dep Apurimac. Andahuaylas, alt. 13000 14000 ft., *Pearce s.n.* (Lectotype: K). **Nototriche pearcei* (E. G. Baker) A. W. Hill, Bot. Jahrb. Syst. **37:** 579. 1906.

M. pedatifidum A. Gray, Boston J. Nat. Hist. **6:** 160, in adn. 1850. TYPE: Texas: near Presidio, on the Rio Grande, *Wright s.n.* (42?) (Holotype: GH; isotype: OXF!). **Sphaeralcea pedatifida* (A. Gray) A. Gray, Proc. Amer. Acad. Arts **22:** 291, in adn. 1887.

M. pedicullariifolium (Meyen) A. Gray, Bot. U. St. Expl. Exped. **1:** 152, in adn. 1854 ("*pedicullariaefolium*"). Basionym: *Sida pedicullariifolia* Meyen, Reise **1:** 460, in adn. 1834 ("*pedicullarifolia*"). TYPE: Peru: Dep. Tacna. high plateau of Tacora near Tissaloma, near pass to Potosì, alt. 4570 m., *Meyen s.n.* (Holotype: B (lost); isotype: K). **Nototriche pedicullariifolia* (Meyen) A. W. Hill, Bot. Jahrb. Syst. **37:** 578. 1906 ("*pedicullarifolia*").

M. pedicullariifolium var. *rugosum* (Philippi) Reiche, Anales Univ Chile **91:** 383. 1895. Basionym: *Malvastrum rugosum* Philippi, Anales Mus. Nac. Chile Bot. **2:** 9. 1891. TYPE: Chile: Prov. Tarapacá, near Machuca, *Philippi 1818a* (Lectotype: SGO no. *41052*; isotype: SGO no. *52013*). **Nototriche rugosa* (Phil.) A. W. Hill, Bot. Jahrb. Syst. **37:** 579. 1906.

M. pennellii Ulbrich, Notizbl. Königl. Bot. Gart. Berlin **11:** 524. 1932. TYPE: Peru: Dep. Arequipa, Arequipa, alt. 2600 2700 m, *Pennell 13206*. Ulbrich stated that the type was at F, but several searches have failed to locate it there. No other examples are known. The description resembles *Urocarpidium* and Ulbrich allied the plant with *Urocarpidium jacens* (S. Wats.) Krap. It is not a *Malvastrum*.

M. pentandrum K. Schumann in Martius, Fl. Bras. **12,** 3: 273. 1892. TYPE: Argentina: Prov. Catamarca. Cuesta de Muschaca, *Schickendantz 305* (Lectotype: B (lost) — photo Field Mus. ser. no. *9321* — F!; isotype: CORD). **Urocarpidium pentandrum* (K. Schumann) Krap., Darwiniana **10:** 632. 1954.

M. pentandrum var. *genuinum* (K. Schumann) Hassler, Feddes Repert. Spec. Nov. Regni Veg. **12:** 496. 1913. Based upon *Malvastrum pentandrum* K. Schumann in Martius, the typical variety, see above. **Urocarpidium pentandrum* (K. Schumann) Krap.

M. pentandrum subsp. *spiciflorum* Hassler. **Malvastrum spiciflorum* (Hassler) Krap. *See text.*

M. peruvianum (Linnaeus) A. Gray, Bot. U. St. Expl. Exped. **1:** 146. 1854. Basionym: *Malva peruviana* Linnaeus, Sp. Pl. **2:** 688. 1753. TYPE: grown at Hortus Uppsaliensis, seeds from de Jussieu (Holotype: LINN microfiche no. *870.5;* isotype: P — Herb. Juss.). **Urocarpidium peruvianum* (L). Krap., Darwiniana **10:** 629. 1954.

M. peruvianum var. *capitatum* Kurtz ex O. Kuntze, Rev. Gen. 3, **2:** 21. 1898, nomen nudum, pro syn. **Tarasa antofagastana* (Phil.) Krap., Bol. Soc. Argent. Bot. **5:** 130. 1954. The Kuntze name applied to *Kurtz s.n.*, Sierra Córdoba, Argentina (GOET, NY).

M. peruvianum var. *elongatum* Hochreutiner, Candollea **15:** 177. 1956. TYPE: Peru: Dep. Ica. Pongo, desert, alt. 500 m., *Rauh & Hirsch P493* (Holotype: G!). **Urocarpidium peruvianum* (L.) Krap., Darwiniana **10:** 629. 1954.

M. peruvianum var. *limense* (Linnaeus) E. G. Baker, J. Bot. **29:** 168. 1891. Basionym: *Malva limensis* Linnaeus, Cent. Pl. **2:** 27. 1756. See *M. limense* above. **Urocarpidium limense* (L.) Krap., Kurtziana **4:** 33. 1967.

M. peruvianum var. *scorpioides* (Turczaninow) E. G. Baker, J. Bot. **29:** 168. 1891. Basionym: *Malva scorpioides* Turczaninow, Bull. Soc. Imp. Naturalistes Moscou **36:** 562. 1863. TYPE: Peru: *Mathews 1006* (Holotype: presumably at KW or CW; isotype: K, OXF!). **Urocarpidium chilense* (Braun & Bouché) Krap., Darwiniana **10:** 619. 1954.

M. peruvianum var. *trisectum* Grisebach, Abh. Königl. Ges. Wiss. Göttingen **19:** 90. 1874. TYPE: Argentina: Prov. Catamarca. Near Yukutula, *Lorentz 671* (Holotype: GOET!; isotypes: CORD, GOET!). **Tarasa trisecta* (Griseb.) Krap., Bol. Soc. Argent. Bot. **5:** 124. 1954.

M. phyllanthos (Cavanilles) A. Gray, Bot. U. St. Expl. Exped. **1:** 152, in adn. 1854. Basionym: *Sida phyllanthos* Cavanilles,

Diss. **5:** 276, t. 127, f. 4. 1788. TYPE: Peru: *de Jussieu s.n.* (Holotype: MA). **Nototriche phyllanthos* (Cav.) A. W. Hill, Bot. Jahrb. Syst. **37:** 579. 1906.

M. pichinchense (Humbolt & Bonpland) A. Gray, Bot. U. St. Expl. Exped. **1:** 152, in adn. 1854. Basionym: *Sida pichinchensis* Humboldt & Bonpland, Voy. Reg. Equin. 6 Bot. sect. 1, **2:** 115, t. 116. 1813. TYPE: Ecuador: Prov. Pichincha, Mt. Rucupichincha, *Bonpland 3032* (Holotype: P). **Nototriche pichinchensis* (Humb. & Bonpl.) A. W. Hill, Bot. Jahrb. Syst. **37:** 579. 1906.

M. pinnatum (Cavanilles) A. Gray, Bot. U. St. Expl. Exped. **1:** 154. 1854. Basionym: *Sida pinnata* Cavanilles, Ic. Pl. **5:** 13, t. 422, f. 1. 1799. TYPE: Ecuador: Prov. Chimborazo, foothills at base of Chimborazo, *Neé s.n.* (Holotype: MA). **Nototriche pinnata* (Cav.) A. W. Hill, Bot. Jahrb. Syst. **37:** 579. 1906.

M. plumosum (Presl) A. Gray, Bot. U. St. Expl. Exped. **1:** 147. 1854. Basionym: *Malva plumosa* Presl, Reliq. Haenk. **2:** 124. 1835. TYPE: Peru: *Haenke s.n.* (Holotype: PR; isotype: W — photo Field Mus. ser. no. *32644*). **Tarasa operculata* (Cav.) Krap., Bol. Soc. Argent. Bot. **5:** 134. 1954.

M. plumosum var. *atacamense* E. G. Baker, J. Bot. **29:** 168. 1891. TYPE: Chile: Atacama desert, *Pearce s.n.* (Holotype: K). **Tarasa operculata* (Cav.) Krap., Bol. Soc. Argent. Bot. **5:** 134. 1954. Considered as such by Bates (1965), but placed in the segregate *Tarasa rahmeri* Philippi, Anales Mus. Nac. Chile Bot.: 10, t. 1, f. 1. 1891, by some.

M. procumbens Harvey in Harvey & Sonder, Fl. Cap. **1:** 164. 1860. TYPE: South Africa: Gamka River, *Burke & Zeyher 89* (Lectotype: K; isotypes: BM, OXF!, PRE, S, TCD). **Anisodontea procumbens* (Harvey in Harv. & Sond.) Bates, Gentes Herb. **10:** 331. 1969.

M. prostratum (Philippi) Hieronymus, Bol. Acad. Nac. Ci. **4:** 15. 1881. Basionym: *Malva prostrata* Philippi, Anales Univ. Chile **35:** 163. 1870, non Cavanilles, 1786. TYPE: Argentina: Mendoza, *Philippi 210* (Lectotype: SGO no. *52171*; isotype: SGO no. *41009*). **Sphaeralcea philippiana* Krap., Lilloa **17:** 199. 1949, based on *Malva prostrata* Philippi.

M. puniceum Jesson, Kew Bull.: 39. 1916. TYPE: Cultivated plant from J. Ross of Ireland. (Holotype: K). **Anisodontea scabrosa* (L.) Bates, Gentes Herb. **10:** 368. 1969.

M. purdiei A. Gray, Bot. U. St. Expl. Exped. **1:** 150, in adn. 1854

("*purdiaei*"). TYPE: Colombia: summit of Páramo Colorado, *Purdie s.n.* (Holotype: GH; isotype: K!). **Acaulimalva purdiei* (A. Gray) Krap., Darwiniana **19:** 26. 1974 ("*purdiaei*").

M. purdiei var. *huantense* E. G. Baker, J. Bot. **29:** 171. 1891. TYPE: Peru: Dep. Ayacucho. Andes of Huanta, alt. 3950–4260 m, *Pearce s.n.* (Holotype: K). **Acaulimalva betonicifolia* (A. W. Hill) Krap., Darwiniana **19:** 16. 1974 ("*betonicaefolia*").

M. purpuratum (Lindley) E. G. Baker, J. Bot. **28:** 370. 1890. Basionym: *Malva purpurata* Lindley, Edward's Bot. Reg.: t. 1362. 1830. TYPE: Raised in 1826 at Kew, Garden of the Horticultural Society, seeds from MacRae, from Cumbre, a pass in the Chilean Andes (Holotype: presumably K, not confirmed; isotype: G!). **Sphaeralcea purpurata* (Lind.) Krap., Lilloa **17:** 218. 1949, a combination based upon t. 1362.

M. purpureum A. W. Hill, J. Linn. Soc. Bot. **39:** 219. 1909. Based upon *Malva purdiei* Weddell, Chlor. And. 2: 275, 1861 ("*purdiaei*"). TYPE: Colombia: summit of Páramo Colorado, *Purdie s.n.* (Holotype: presumably P; isotype: K!). **Acaulimalva purpurea* (A. W. Hill) Krap., Darwiniana **19:** 27. 1974. Nomenclaturally but not taxonomically confused; see discussion in A. W. Hill (1909) cited above, and *M. purdiei.*

M. pygmaeum sensu Grisebach, Abh. Königl. Ges. Wiss. Göttingen **24:** 43. 1879. **Tarasa tenella* (Cav.) Krap., Bol. Soc. Argent. Bot. **5:** 123. 1954.

M. pygmaeum (Remy) E. G. Baker, J. Bot. **29:** 167. 1891. Basionym: *Sida pygmaea* Remy, Ann. Sci. Nat. Bot. ser. 3, **8:** 238. 1847. TYPE: Bolivia: Dep. Tacna, near Laguna de Potosi, alt. 4200–4300 m., *D'Orbigny 1359* (Holotype: P — photo Field Mus. ser. no. *35509* — F!). **Nototriche pygmaea* (Remy) A. W. Hill, Trans. Linn. Soc. London **7:** 218. 1909.

M. racemosum Harvey in Harvey & Sonder, Fl. Cap. **1:** 163. 1860. Based on *Malva racemosa* E. Meyer in Drége, Zwei Pflanz. Docum. **70:** 201. 1843, nom. nud., non Presl. 1822. TYPE: South Africa: Cape Province, Clanwilliam Dist., between Grasberg River and Waterval, alt. 2500–3000 ft., *Drége s.n.* (Lectotype: K; isotypes: G!, MO, OXF!, P). **Anisodontea racemosa* (Harv. in Harv & Sond.) Bates, Gentes Herb. **10:** 351. 1969.

M. rauhii Hochreutiner, Candollea **16:** 77. 1957. TYPE: Peru: Dep. Junín, Ticllo, puna, alt. 4800 m., *Rauh & Hirsch P261* (Lectotype: G!; Isotype: G!). **Acaulimalva rauhii* (Hochr.) Krap., Darwiniana **19:** 28. 1974.

M. retusum (Cavanilles) E. G. Baker, J. Bot. **28:** 370. 1890. Basionym: *Malva retusa* Cavanilles, Diss. **2:** 73, t. 21, f. 1. 1786. TYPE: South Africa: Cape of Good Hope, *Sonnerat s.n.* (Holotype: MA). **Anisodontea scabrosa* (L.) Bates, Gentes Herb. **10:** 368. 1969.

M. rhizanthum A. Gray, Bot. U. St. Expl. Exped. **1:** 148. 1854. TYPE: Peru: above Baños, *Pickering s.n.* (Holotype: US no. *15210!*). **Acaulimalva rhizantha* (A. Gray) Krap., Darwiniana **19:**31. 1974.

M. ribifolium (Schlechtendal) Hemsley, Biol. Centr. Amer. Bot. **1:** 100. 1879. Basionym: *Malva ribifolia* Schlechtendal, Linnaea **11:** 351. 1837, non Viv., 1825. TYPE: Mexico: Mineral del Monte, *Ehrenberg 283* (Holotype: HAL no. *43664* !; isotype: B (lost) — photo Field Mus. ser. no. *323*). **Kearnemalvastrum subtriflorum* (Lag.) Bates, Brittonia **19:** 232. 1967.

M. richii A. Gray, Bot. U. St. Expl. Exped. **1:** 149. 1854. TYPE: Peru: Dep. Junín, near Obrajillo or Baños, Andes, *Pickering s.n.* (Holotype: US!). **Acaulimalva richii* (A. Gray) Krap., Darwiniana **19:** 32. 1974.

M. riparium Hutchinson, Botanist in S. Afr.: 106, in adn. 1946. TYPE: South Africa: Caledon Dist. Near stream bed east of Bot River, *Hutchinson 489* (Holotype: K; isotypes: BM, BCL, PRE). **Anisodontea scabrosa* (L.) Bates, Gentes Herb. **10:**368. 1969.

M. roseum (De Candolle) Hemsley, Biol. Centr. Am. Bot. **1:** 100. 1879. Basionym: *Malva rosea* De Candolle, Prodromus **1:** 435. 1824. TYPE: Calque des Dessins de la Flore du Mexique de Mociño et Sessé . . ., plate no. 58 (F,G,US). The unpublished plates have been cited by Fryxell, Madroño **21:** 168. 1971. **Phymosia rosea* (DC.) Kearney, Leafl. W. Bot. **5:** 190. 1949.

M. rotundifolium A. Gray, Proc. Amer. Acad. Arts **7:** 333. 1868. TYPE: California: sand hills at Fort Mohave, *Cooper s.n.* (Holotype: GH; isotype: K, US!). **Eremalche rotundifolia* (A. Gray) Greene, Leafl. Bot. Observ. Crit. **1:** 208. 1906.

M. ruderale Hance ex Walpers. **Malvastrum coromandelianum* (L.) Garcke subsp. *coromandelianum. See text.*

M. rugelii S. Watson. **Malvastrum corchorifolium* (Desr. in Lam.) Britton ex Small. *See text.*

M. rugosum Philippi, Anales Mus. Nac. Chile Bot. **2:** 9, 1891. See *M. pedicullariifolium* var. *rugosum* above. **Nototriche rugosa* (Phil.) A. W. Hill.

M. rusbyi Britton, Bull. Torrey Bot. Club **16:** 64. 1889. TYPE: Bolivia: Near La Paz, alt. 10,000 ft. *Rusby 1780* (Lectotype: NY; isotypes: MICH! ND, PH! US!). **Tarasa capitata* (Cav.) Bates, Gentes Herb. **9:** 388. 1965.

M. sajamense Hieronymus, Bot. Jahrb. Syst. **21:** 319, 1896. TYPE: Peru: Dep. Tacna. Tacora mountains, alt. 4500 4800 m, *Stübel 108* (Holotype: B (lost); isotype: K). **Nototriche sajamensis* (Hieron.) A. W. Hill, Bot. Jahrb. Syst. **37:** 579. 1906.

M. saltense Hieronymus ex O. Kuntze, Rev. Gen. 3, **2:** 22. 1898, nomen nudum, non Hieron. ex Fries 1905. Later named **Nototriche saltensis* A. W. Hill, Bot. Jahrb. Syst. **37:** 587. 1906, based on *Hieronymus & Niederlein 41.*

M. saltense Hieronymus ex R. E. Fries, Nova Acta Regiae Soc. Sci. Upsal. ser. 4, **1:** 127. 1905, non Hieron. ex O. Ktze., 1898, nomen nudum. This name was attributed to K. Schumann by Hill (1909b), who stated that it applied to **Nototriche anthemidifolia* (Remy) A. W. Hill, Bot. Jahrb. Syst. **37:** 578. 1906.

M. sandemannii Sandwith, Kew Bull.: 263. 1950. TYPE: Peru: Dep. Arequipa. Chala, alt. 500 m. *Sandemann 4020* (Holotype: K!; isotype: OXF!). **Modiolastrum sandemannii* (Sandw.) Hill & Fryxell, Brittonia **32**(4): 484. 1980.

M. scabrosum (Linnaeus) Stapf. Bot. Mag. **151:** t. 9087. 1925. Basionym: *Malva scabrosa* Linnaeus, Cent. 2 Plant.: 27. 1756. TYPE: Lectotype chosen by Bates (1969) is t. 86, Commelin, Horti Medici. Amstelod. descr. 171, t. 86. 1701. **Anisodontea scabrosa* (Linnaeus) Bates, Gentes Herb. **10:** 368. 1969.

M. scabrum (Cavanilles) A. Gray. **Malvastrum tomentosum* (L.) S. R. Hill. *See text.*

M. scabrum var. *amblyphyllum* (R. E. Fries) Hassler. **Malvastrum amblyphyllum* R. E. Fries. *See text.*

M. scabrum var. *genuinum* Hassler. The typical variety. **Malvastrum tomentosum* (L.) S. R. Hill. *See text.*

M. scabrum var. *paraguariense* Hassler. **Malvastrum amblyphyllum* R. E. Fries. *See text.*

M. scabrum var. *tucumanense* Hassler. **Malvastrum amblyphyllum. See text.*

M. schaffneri S. Watson, Proc. Amer. Acad. Arts **25:** 143. 1890. TYPE: Mexico: Est. Coahuila. Carneros Pass, *Pringle 2849* (Lectotype: GH; isotypes: BKL! F! NY! US! VT!). **Kearnemalvastrum subtriflorum* (Lag.) Bates, Brittonia **19:** 232. 1967.

**M. scoparioides* Ulbrich. *See text.*

M. scoparium (L'Heritier) A. Gray. **Malvastrum tomentosum* (L.) S. R. Hill. *See text.*

M. scorpioides (O. Kuntze) K. Schumann, Bot. Jahresber. (Just) **26:** 355. 1898. Basionym: *Malveopsis scorpioides* O. Kuntze, Rev. Gen. 3, **2:** 22. 1898. TYPE: Bolivia: Río Tapacari, alt. 3000 m., (?) *Kuntze s.n.* (Holotype: NY!; isotype: US!). This is a *Tarasa,* but Krapovickas (1954, p. 142) has not assigned it to a species in that genus due to its lack of mature fruits.

M. setosum Harvey in Harvey & Sonder, Fl. Cap. **1:** 163. 1860. TYPE: South Africa: Piquetberg Dist. At Piquetberg near Groenvalei, alt. less than 1000 ft., *Drége 7231* (Lectotype: K; isotypes: G!, L, MO, P). **Anisodontea setosa* (Harvey) Bates, Gentes Herb. **10:** 344. 1969.

M. shepardae I. M. Johnston, Contr. Gray Herb. n. s. **70:** 75. 1924. TYPE: Peru: in meadows, Puno, alt. 3125 m., *Shepard 123* (Holotype: GH). **Urocarpidium shepardae* (I. M. Johnst.) Krap., Darwiniana **10:** 621. 1954.

M. spicatum (Linnaeus) A. Gray. **Malvastrum americanum* (L.) Torrey in Emory. *See text.*

M. spicatum var. *mollissima* Chevalier. **Malvastrum americanum* (L.) Torrey in Emory. *See text.*

**M. spiciflorum* (Hassler) Krapovickas. *See text.*

M. splendidum Kellogg, Proc. Calif. Acad. Sci. **1:** 67. 1855. See *M. fasciculatum* var. *laxiflorum.* **Malacothamnus fasciculatus.* (Nutt. ex Torr. & Gray) Greene var. *laxiflorus* (A. Gray) Kearney.

M. splendidum sensu Davidson, Erythea **4:** 68. 1896. **Malacothamnus davidsonii* (Robinson) Greene, Leafl. Bot. Observ. Crit. **1:** 208. 1906. See *M. davidsonii* above and *M. splendidum* below.

M. splendidum Davidson ex Robinson in A. Gray, Syn. Fl. N. Am. 1, **1:** 312. 1897, pro syn., nom. nud. **Malacothamnus davidsonii* (Robinson) Greene. See *M. davidsonii* and *M. splendidum* above.

M. stenopetalum A. Gray, Bot. U. St. Expl. Exped. **1:** 155. 1854. TYPE: Peru: Dep. Lima. Alpine Cordilleras near Casa Cancha, *Pickering s.n.* (Holotype: US). **Nototriche stenopetala* (A. Gray) A. W. Hill, Bot. Jahrb. Syst. **37:** 579. 1906.

M. stipulare Philippi, Anales Mus. Nac. Chile Bot. **2:** 8. 1891. TYPE: Chile: Prov. Tarapacá, Machuca, alt. 3200 m, *Philippi s.n.* (Holotype: SGO no. *52009;* isotype: GH). This is a *Nototriche,* but has not been studied in detail.

M. strictum (Jacquin) Gray & Harvey in Harvey & Sonder, Fl. Cap. **1:** 161. 1860. Basionym: *Malva stricta* Jacquin, Hort. Schoenbr. 3: 24, t. 294. 1789. TYPE: t. 294 was chosen as lectotype by Bates (1969, p. 370). **Anisodontea scabrosa* (L.) Bates, Gentes Herb. **10:** 368. 1969.

M. stuebellii Hieronymus, Bot. Jahrb. Syst. **21:** 318. 1896. TYPE: Peru: Dep. Cajamarca. Near Cajamarca, monte Altura de Santa Ursula, *Stübel 38* (Holotype: B (lost) — photo Field Mus. ser. no. *9325* — F!). **Acaulimalva stuebelii* (Hieron.) Krap., Darwiniana **19:** 34. 1974.

M. subacaule (Philippi) E. G. Baker, J. Bot. **32:** 36. 1894. Basionym: *Malva subacaulis* Philippi, Anales Univ. Chile **82:** 14. 1893, non Coss. ex Baker, J. Bot. **28:** 340. 1890. See *M. humile* var. *subacaule* above. **Tarasa humilis* (Gill. ex Hook. & Arn.) Krap.

M. subtriflorum (Lagasca) Hemsley, Biol. Centr. Am. Bot. **1:** 100. 1879. Basionym: *Malva subtriflora* Lagasca, Elenchus Pl.: 21. 1816. TYPE: Plant cultivated at the Royal Botanic Garden Madrid, seeds sent by Sessé (Holotype: presumably MA). **Kearnemalvastrum subtriflorum* (Lag.) Bates, Brittonia **19:** 232. 1967.

M. sulphureum (Gillies ex Hooker & Arnott) Grisebach, Abh. Königl. Ges. Wiss. Göttingen **24:** 43. 1879 ("*sulfureum*"). Basionym: *Malva sulphurea* Gillies ex Hooker & Arnott, Bot. Misc. **3:** 149. 1833. TYPE: Argentina: Mendoza, roadside and about houses, *Gillies s.n.* (Holotype: K; isotype: OXF!). **Malvella leprosa* (Ort.) Krap., Bonplandia **3:** 59. 1970.

M. tarapacanum (Philippi) E. G. Baker, J. Bot. **28:** 371. 1890, nomen nudum. A combination based on the nomen nudum *Malva tarapacana* Philippi ex E. G. Baker, J. Bot. **28:** 371. 1890. See *M. tarapacanum* below.

M. tarapacanum (Philippi) E. G. Baker, J. Bot. **29:** 167. 1891. A new combination made valid by the publication of the basionym: *Malva tarapacana* Philippi, Anales Mus. Nac. Chile Bot. **2:** 8. 1891. TYPE: Chile: Prov. Tarapacá, Jaiña, *Rahmer s.n.* (Lectotype: SGO no. *41025*; isotypes: B (lost) — photo Field Mus. ser.

no. *9326* — F! G! K, SGO no. *51990*). **Tarasa tarapacana* (Philippi) Krap., Bol. Soc. Argent. Bot. **5:** 121. 1954.

M. tenellum (Cavanilles) Hieronymus, Bol. Acad. Nac. Ci. **4:** 16. 1881. Basionym: *Malva tenella* Cavanilles, Icones Pl. **5:** 14, t. 422, f. 3. 1799. TYPE: Chile: Cordillera, ?*Nee* (Holotype: presumably MA). **Tarasa tenella* (Cav.) Krap., Bol. Soc. Argent. Bot. **5:** 123. 1954, based upon t. 422, f. 3.

M. tenuifolium E. G. Baker, J. Bot. **28:** 371. 1890. Based on: *Malva tenuifolia* Hooker & Arnott, Bot. Misc. **3:** 150. 1833, non Savi, 1804. Nom. illegit. TYPE: Chile: Prov. Maule, *Cuming 841* (Holotype: K). **Sphaeralcea purpurata* (Lindley) Krap., Lilloa **17:** 218. 1949.

M. thurberi A. Gray, Mem. Amer. Acad. Arts n.s. 2, **5:** 307. 1855. TYPE: Mexico: Est. Sonora. Valley near Santa Cruz, *Thurber 709* (Holotype: GH — fragment F!; isotypes: F!, GH, MO, NY). **Malacothamnus fasciculatus* (Nutt. ex Torr. & Gray) Greene subsp. *fasciculatus*, Leafl. Bot. Observ. Crit. **1:** 208. 1906. Bates (1963, ined.) raised some question as to the correct location cited for the type.

M. thurberi var. *laxiflorum* A. Gray, Proc. Amer. Acad. Arts **22:** 291, in adn. 1887. See *M. fasciculatum* var. *laxiflorum* and *M. laxiflorum* above. **Malacothamnus fasciculatus* (Nutt. ex Torr. & Gray) Greene var. *laxiflorus* (A. Gray) Kearney.

M. trachelifolium (Link) Ulbrich. **Malvastrum americanum* (L.) Torrey in Emory. See text.

M. tricuspidatum (R. Brown in Aiton) A. Gray. **Malvastrum coromandelianum* (L.) Garcke. *See text.*

M. tricuspidatum var. *bicuspidatum* S. Watson. **Malvastrum bicuspidatum* (S. Wats.) Rose subsp. *bicuspidatum. See text.*

M. tricuspidatum var. *capitato-spicatum* (O. Kuntze) Stuckert. **Malvastrum coromandelianum* (L.) Garcke subsp. *capitato-spicatum* (O. Kuntze) S. R. Hill. *See text.*

M. tricuspidatum var. *congestum* (R. E. Fries) Stuckert. **Malvastrum coromandelianum* (L.) Garcke subsp. *capitato-spicatum* (O. Kuntze) S. R. Hill. *See text.*

M. tricuspidatum var. *normale* (O. Kuntze) Stuckert. **Malvastrum coromandelianum* (L.) Garcke subsp. *coromandelianum. See text.*

M. tridactylides (Cavanilles) Gray & Harvey in Harvey & Sonder,

Fl. Cap. **1:** 162. 1860 ("*tridactylites*"). Basionym: *Malva tridactylides* Cavanilles, Diss. **2:** 73, t. 21, f. 2. 1786. TYPE: South Africa: Cape of Good Hope, *Sonnerat s.n.* (Holotype: MA; isotypes: P, P-LA). **Anisodontea fruticosa* (Bergius) Bates, Gentes Herb. **10:** 348. 1969.

M. tridactylides var. *α glabrum* Harvey in Harvey & Sonder, Fl. Cap. 1: 162, 1860 ("*glabra*"). TYPE: South Africa: Worcester Dist. In mountains near Tulbagh, *Ecklon & Zeyher 283* (Lectotype: S). **Anisodontea fruticosa* (Bergius) Bates, Gentes Herb. **10:** 348. 1969.

M. tridactylides var. *β puberulum* Harvey in Harvey & Sonder, Fl. Cap. **1:** 162. 1860 ("*puberula*"). TYPE: South Africa: Swellendam Dist. near Hassaquaskloof and Breederivier, *Ecklon & Zeyher 292* (Lectotype: S; isotypes: C, G!, K, L, MO, NBG, P, S). **Anisodontea fruticosa* (Bergius) Bates, Gentes Herb. **10:** 348. 1969.

M. tridactylides var. *setosum* (Harvey) Garcke, Bot. Zeitung **22:** 11. 1864. Basionym: *Malvastrum setosum* Harvey in Harvey & Sonder, see above. **Anisodontea setosa* (Harvey) Bates, Gentes Herb. **10:** 344. 1969.

M. tridactylides var. *γ stellulatum* Harvey in Harvey & Sonder, Fl. Cap. **1:** 162. 1860 ("*stellulata*"). TYPE: South Africa Swellendam Dist. near Hassaquaskloof and Breederivier. *Ecklon & Zeyher 292* (Neotype: S; isotypes: C, G, K, L, MO, NBG, P, S). See discussion in Bates, (1969, p. 348). **Anisdontea fruticosa* (Bergius) Bates, Gentes Herb. **10:** 348. 1969.

M. trilobatum E. G. Baker, J. Bot. **29:** 164, 1891. TYPE: South Africa: Cape Province. George Distr., *Alexander & Prior s.n.* (Holotype: BM; isotype: K). **Anisodontea scabrosa* (L.) Bates, Gentes Herb. **10:** 368. 1969.

M. trilobum (Thunberg) Garcke, Bot. Zeitung **22:** 11. 1864. Basionym: *Malva triloba* Thunberg, Prodr. Pl. Cap.: 118. 1800, non Cavanilles, 1803. TYPE: South Africa: Karro and Cannaland, *Thunberg s.n.* (Holotype: UPS — microfiche no. *16019*). **Anisodontea triloba* (Thunb.) Bates, Gentes Herb. **10:** 363. 1969.

M. tuberculatum A. W. Hill, Kew Bull.: 486. 1933. TYPE: Argentina: Prov. Catamarca, Dep. Andalgalá, *Jörgensen 1346* (Holotype: K!; isotype: BA, GH). **Acaulimalva nubigena* (Walpers) Krap., Darwiniana **19:** 22. 1974.

M. tweedii E. G. Baker, J. Bot. **29:** 169. 1891. TYPE: Uruguay, *Tweedie s.n.* (Holotype: K). **Modiolastrum malvifolium* (Griseb.) K. Schumann in Martius, Fl. Bras. 12, **3:** 277. 1891.

M. ulophyllum A. Gray, Bot. U. St. Expl. Exped. **1:** 150. 1854. TYPE: Peru: Alpine Cordilleras at Alpamarca near the snow line, *Pickering s.n.* (Holotype: US no. *15211*!). **Nototriche ulophylla* (A. Gray) A. W. Hill, Bot. Jahrb. Syst. **37:** 579. 1906.

M. urbanianum Ulbrich, Bot. Jahrb. Syst. **42:** 119. 1909. TYPE: Peru: Prov. Sandia above Cuyocuyo, alt. 3600–3800 m., *Weberbauer 927* (Holotype: B (lost) - photo Field Mus. ser. no. *9327* — F!; isotype: USM). **Tarasa urbaniana* (Ulbrich) Krap., Bol. Soc. Argent. Bot. **5:** 140. 1954.

M. violaceum (Philippi) Hieronymus, Bol. Acad. Nac. Ci. **4:** 15. 1881. Basionym: *Malva violacea* Philippi, Anales Univ. Chile **35:** 162. 1870. TYPE: Argentina: Mendoza, *Philippi s.n.* (Holotype: SGO no. *41008*). **Sphaeralcea brevipes* (Phil.) Krap., Lilloa 17: 196, 1949.

M. virgatum (Murray) Gray & Harvey in Harvey & Sonder, Fl. Cap. **1:** 162. 1860. Basionym: *Malva virgata* Murray, Comment. Soc. Regiae Sci. Gott. **2:** 20, t. 6. 1779. TYPE: Cultivated specimen from Hort. Cliffordianus (Holotype: BM — Clifford Herbarium). **Anisodontea capensis* (L.) Bates, Gentes Herb. **10:** 327. 1969.

M. virgatum sensu Gray & Harvey in Harvey & Sonder, Fl. Cap. **1:** 162. 1860, excl. basionym. **Anisodontea scabrosa* (L.) Bates, Gentes Herb. **10:** 368. 1969.

M. virgatum var. *β angustifolium* Harvey in Harvey & Sonder, Fl. Cap. **1:** 162. 1860 ("*angustifolia*"). See *M. angustifolium* (Harvey) Stapf ex Fourcade above. **Anisodontea scabrosa* (L.) Bates.

M. virgatum var. *α dillenianum* (Ecklon & Zeyher) Harvey in Harvey & Sonder, F. Cap. **1:** 162. 1860 ("*dilleniana*"). Basionym: *Malva dilleniana* Ecklon & Zeyher, Enum. Pl. Afr. Aust. Extratrop.: 36. 1834. TYPE: Bates (1969) selected f. 206 in Dillenius, Hort. Eltham. 2: 108, t. 169, f. 206. 1732. **Anisodontea capensis* (L.) Bates, Gentes Herb. **10:** 327. 1969.

M. virgatum var. *α dillenianum* sensu Harvey in Harvey & Sonder, Fl. Cap. **1:** 162. 1860, excl. basionym. **Anisodontea scabrosa* (L.) Bates, Gentes Herb. **10:** 368. 1969.

M. virgatum var. *oblongifolium* Harvey in Harvey & Sonder, Fl. Cap. **1:** 162. 1860. TYPE: South Africa: *Drége 7318b* (Holotype: K; isotypes: MO, P). **Anisodontea scabrosa* (L.) Bates, Gentes Herb. **10:** 368. 1969.

M. viscidum Abrams, Bull. Torrey Bot. Club **34:** 264. 1907. See *M. densiflorum* var. *viscidum* above. **Malacothamnus densiflorus* (S. Wats.) Greene var. *viscidus* (Abrams) Kearney.

M. vitifolium (Cavanilles) Hemsley, Biol. Centr. Am. Bot. **1:** 100. 1879. Basionym: *Malva vitifolia* Cavanilles, Icon. Pl. **1:** 13, t. 20. 1791, non Cervant. ex Steud, 1841, nom. nud. TYPE: Cultivated plant at the Royal Botanic Garden Madrid (Holotype: MA — photo BH neg. *15651* and US neg. *451*). **Kearnemalvastrum lacteum* (Ait.) Bates, Brittonia **19:** 231. 1967.

M. waltheriifolium (Link) Ulbrich. **Malvastrum tomentosum* (L.) S. R. Hill. *See text.*

M. weberbaueri Ulbrich, Bot. Jahrb. Syst. **42:** 115. 1909. TYPE: Peru: Dep. Ancash. Prov. Cajatambo, above Ocros in fields, alt. 3500–3600 m, *Weberbauer 2760* (Holotype: B (lost) — photo Field Mus. ser. No. *9328* — F!, fragment of holotype at K!; isotypes: G! MOL). **Acaulimalva weberbaueri* (Ulbr.) Krap., Darwiniana **19:** 35. 1974.

M. wilczekii Hochreutiner var. *genuinum* Hochreutiner, Annuaire Conserv. Jard. Bot. Genève **21:** 424, f. 26. 1920. TYPE: Argentina: Prov. Mendoza, San Rafael, *Wilczek 290* (Holotype: G! — photo Field Mus. ser. no. *23737* — F!; isotype: LAU!). **Sphaeralcea mendocina* Philippi, Anales Univ. Chile **2:** 392. 1862.

M. wilczekii var. *macrocarpum* Hochreutiner, Annuaire Conserv. Jard. Bot. Genève **21:** 426. 1920. TYPE: Argentina: Prov. Mendoza, San Rafael, *Wilczek 289* (Holotype: G; isotype: LAU!). **Sphaeralcea mendocina* Philippi, Anales Univ. Chile **2:** 392. 1862.

M. wrightii A. Gray. **Malvastrum aurantiacum* (Scheele) Walpers. *See text.*

THE COMPOSITION, SEASONAL OCCURRENCE AND REPRODUCTIVE PERIODICITY OF THE PHAEOPHYCEAE (BROWN ALGAE) IN NEW HAMPSHIRE[1]

ARTHUR C. MATHIESON AND EDWARD J. HEHRE[2]

Until recently there have been few published accounts of the marine algae of New Hampshire (Farlow, 1881; Collins, 1900, 1901, 1903, 1906; Croasdale, 1941; Wood & Straughan, 1953; Doty & Newhouse, 1954). However, since the mid 1960's we have conducted a variety of floristic and ecological investigations of New Hampshire seaweeds in order to interpret better their diversity, distribution, and abundance. In the present account we attempt to summarize all known records of brown algae from New Hampshire with four primary objectives as follows: (1) to describe the species composition of the brown algae in New Hampshire; (2) to record their seasonal occurrences; (3) to determine, where possible, species reproductive periodicities, and; (4) to characterize their local distribution within coastal and estuarine habitats.

STUDY AREA AND METHODS

Seasonal collections and observations of littoral and sublittoral brown algae in New Hampshire were made at numerous coastal and estuarine sites (Table I) from 1965-1980. Detailed habitat descriptions of several of the collecting sites, as well as general accounts of the New Hampshire coastal zone are given elsewhere (e.g. Hehre & Mathieson, 1970; Mathieson & Fralick, 1972; Mathieson, Hehre, & Reynolds, 1981; Mathieson, Reynolds, & Hehre, 1981; Norall & Mathieson, 1976). Two major open coastal and two primary estuarine areas occur within the state (Figs. 1 and 2, Table I): (1) the Isles of Shoals, an interstate set of islands which are located approximately 9 miles SSE of Portsmouth; four of these islands are in New

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Table I Summary of collection sites

Geographical Area	Number and/or names of permanent stations	Sites with at least 2 years of seasonal collections	Sites with at least 2 years of monthly collections	Pertinent references
(1) Isles of Shoals	Anderson Ledge	×		Mathieson 1979
	Appledore Island	×		
	Cedar Island	×		
	Duck Island	×		
	Lunging Island	×		
	Malaga Island	×		
	Smuttynose Island	×		
	Star Island	×		
	White Island	×		
(2) Nearshore open coast from Portsmouth to Seabrook	14 sites		×	
	Jaffrey Point, Newcastle (70° 42′49″ W, 43° 03′22″ N)		×	Mathieson, Hehre, & Reynolds, 1981
	Bound Rock, Seabrook (70° 48′45″ W, 42° 53′30″ N)		×	Daly and Mathieson 1977

(3) Hampton-Seabrook Estuary System	49 total sites	×		Mathieson & Fralick 1972
	Blackwater River – 11 sites	×		
	Brown River – 13 sites	×		
	Hampton River – 18 sites	×		
	Hampton Harbor – 7 sites	×		
(4) Great Bay Estuary System	166 total sites	×		Mathieson, Reynolds, & Hehre, 1981
	Great Bay – 16 sites	×		
	Crommet Creek, Durham (70° 53′ W, 43° 05′52″ N)		×	
	Nannies Island, Newington (70° 51′47″ W, 43° 04′08″ N)		×	
	Thomas Point, Newington (70° 51′56″ W, 43° 04′53″ N)		×	
	Weeks Point, Greenland (70° 51′42″ W, 43° 03′32″ N)		×	
	Little Bay – 21 sites	×		
	Adams Point, Durham (70° 52′07″ W, 43° 05′43″ N)		×	
	Cedar Point, Durham (70° 51′08″ W, 43° 07′45″ N)		×	Chock & Mathieson, 1976, in press
	Dover Point, Dover (70° 49′42″ W, 43° 07′07″ N)		×	Reynolds and Mathieson, 1975
	Durham Point, Durham (70° 52′10″ W, 43° 07′14″ N)		×	Mathieson, et. al., 1977
	Bellamy River – 10 sites	×		
	Cocheco River – 17 sites	×		

Table I Continued

Geographical Area	Number and/or names of permanent stations	Sites with at least 2 years of seasonal collections	Sites with at least 2 years of monthly collections	Pertinent references
	Lamprey River – 9 sites	×		
	Oyster River – 14 sites	×		
	Headwater at route 108 Durham (70°55′06″ W, 43°07′52″ N)		×	
	Piscataqua River – 59 sites	×		
	Atlantic Heights, Portsmouth (70°46′08″ W, 43°05′36″ N)			Mathieson et al. 1977
	Normandeau Schiller site #16, just east of the Schiller Power generating station (70°46′51″ N, 43°05′41″ W)		8 years of continuous seasonal collections	
	ibid. #17, at end of Long Reach Farm, Eliot, Maine (70°46′52″ W, 43°06′02″ N)		8 years of continuous seasonal collections	
	ibid. #20, near Schiller Power Plant, Newington (70°47′47″ W, 43°06′15″ N)		8 years of continuous seasonal collections	

ibid. #40, near Simplex Pier, Newington (70°47′47″ W, 43°06′15″ N)		8 years of continuous seasonal collections
ibid. #44, area just west of Simplex Pier and Union Oil Terminal, Newington (70°47′58″ W, 43°06′28″ N)		8 years of continuous seasonal collections
Salmon Falls River		
Squamscott River	×	
16 sites		
Chapman's Landing (70°55′43″ W, 43°02′24″ N)		×
Winnicut River		
4 sites	×	

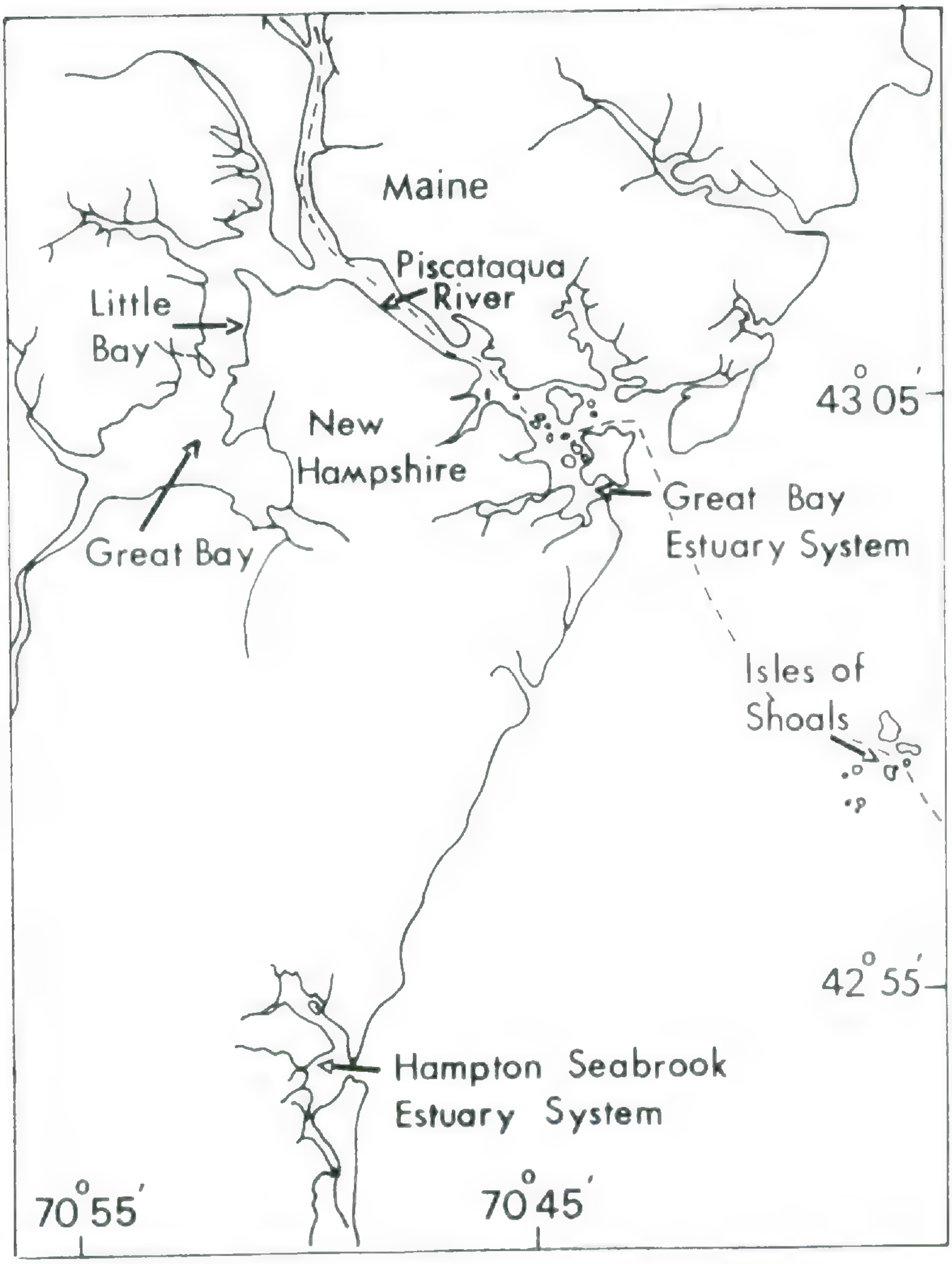

Figure 1. The New Hampshire coastal zone

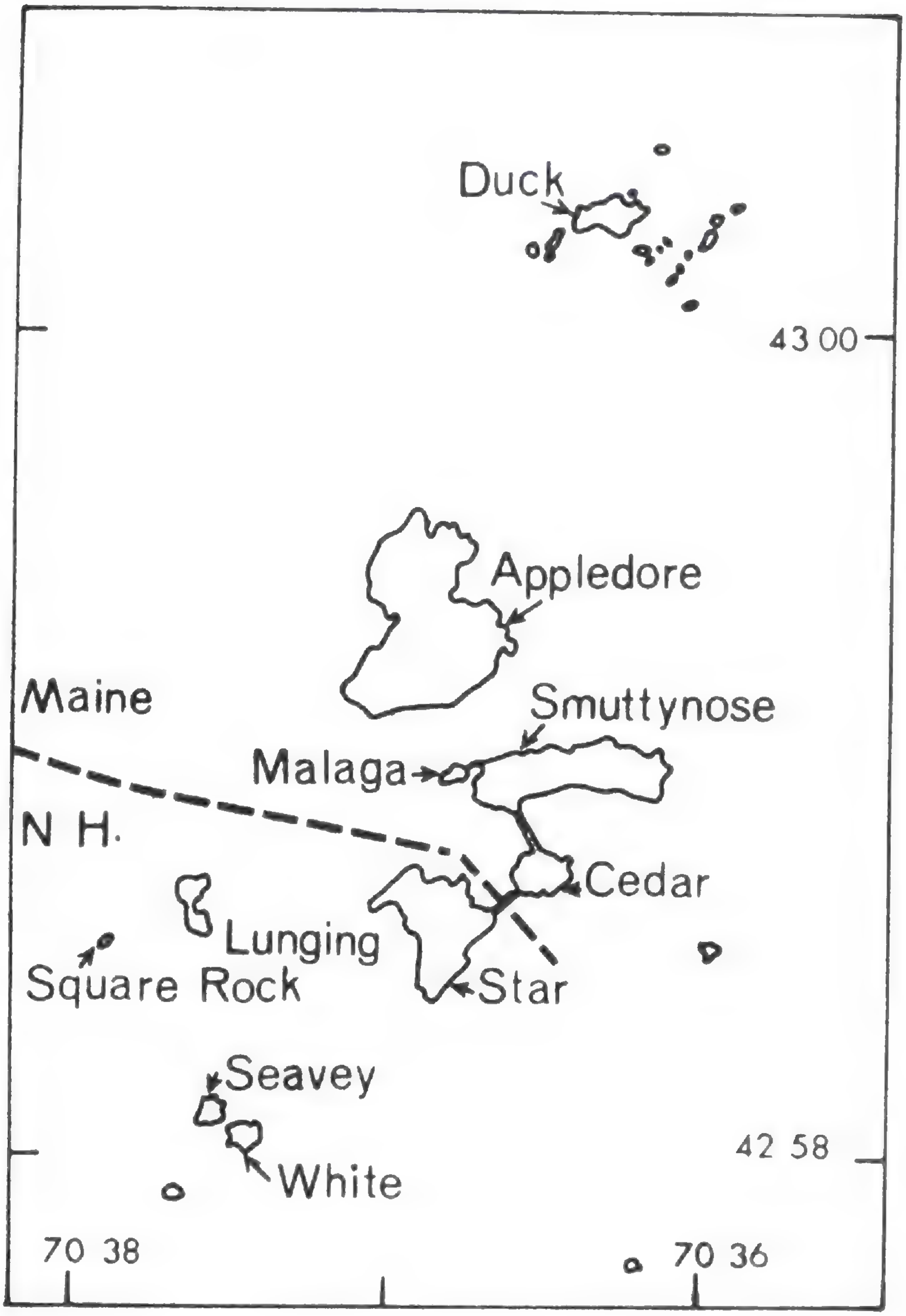

Figure 2. The Isles of Shoals, New Hampshire — Maine

Hampshire (i.e. Lunging, Seavey, Star, and White; (2) the nearshore open coast and adjacent salt marshes between Seabrook and Portsmouth; (3) the Hampton-Seabrook Estuary System that includes Hampton Harbor and three major tributaries (i.e. the Blackwater, Brown, and Hampton Rivers); (4) the Great Bay Estuary System that includes Great Bay, Little Bay, the Piscataqua River, and seven other major tributaries (Bellamy, Cocheco, Lamprey, Oyster, Salmon Falls, Squamscott, and Winnicut Rivers).

Specimens were collected either on foot within the littoral zone (Lewis, 1964) or by SCUBA diving within the sublittoral zone (Mathieson, 1979). Samples were brought to the laboratory (fresh) for identification, determination of reproductive structures, and processing of voucher specimens. The nomenclature of South (1976) was applied in most cases. Herbarium voucher specimens of each taxon were prepared from a wide variety of sites, either monthly or seasonally, and deposited in the Albion R. Hodgdon Herbarium of the University of New Hampshire (NHA).

PHENOLOGY AND DISTRIBUTION

Figure 3, which is based upon the data in Table II, illustrates the monthly occurrence and reproduction of phaeophycean taxa within the state. The number of taxa/month showed a pronounced seasonal pattern. The lowest numbers of brown algae were recorded in December and January, while the highest were noted in August. Reproductive levels of brown algae were highest in late fall-winter and lowest in the summer. Thus, the highest levels of reproduction occurred when the lowest number of taxa were recorded while the opposite reproductive pattern was apparent during periods of highest species numbers. In comparing the seasonal occurrence of the phaeophycean flora, 30 taxa (45%) were considered to be perennials, while 36 taxa (55%) were interpreted as annuals (Fig. 4). Details on longevity and seasonal occurrence are summarized in Table II and in the following annotated checklist.

A summary of the local distribution of phaeophycean taxa in the four major coastal-estuarine areas in New Hampshire is shown in Figure 4. The highest diversity of brown algae was found at the two open coastal areas, with 47 taxa occurring at the Isles of Shoals and 48 taxa from the 18 miles of open coast between Seabrook and Portsmouth. In contrast, 36 taxa were collected from the Great Bay

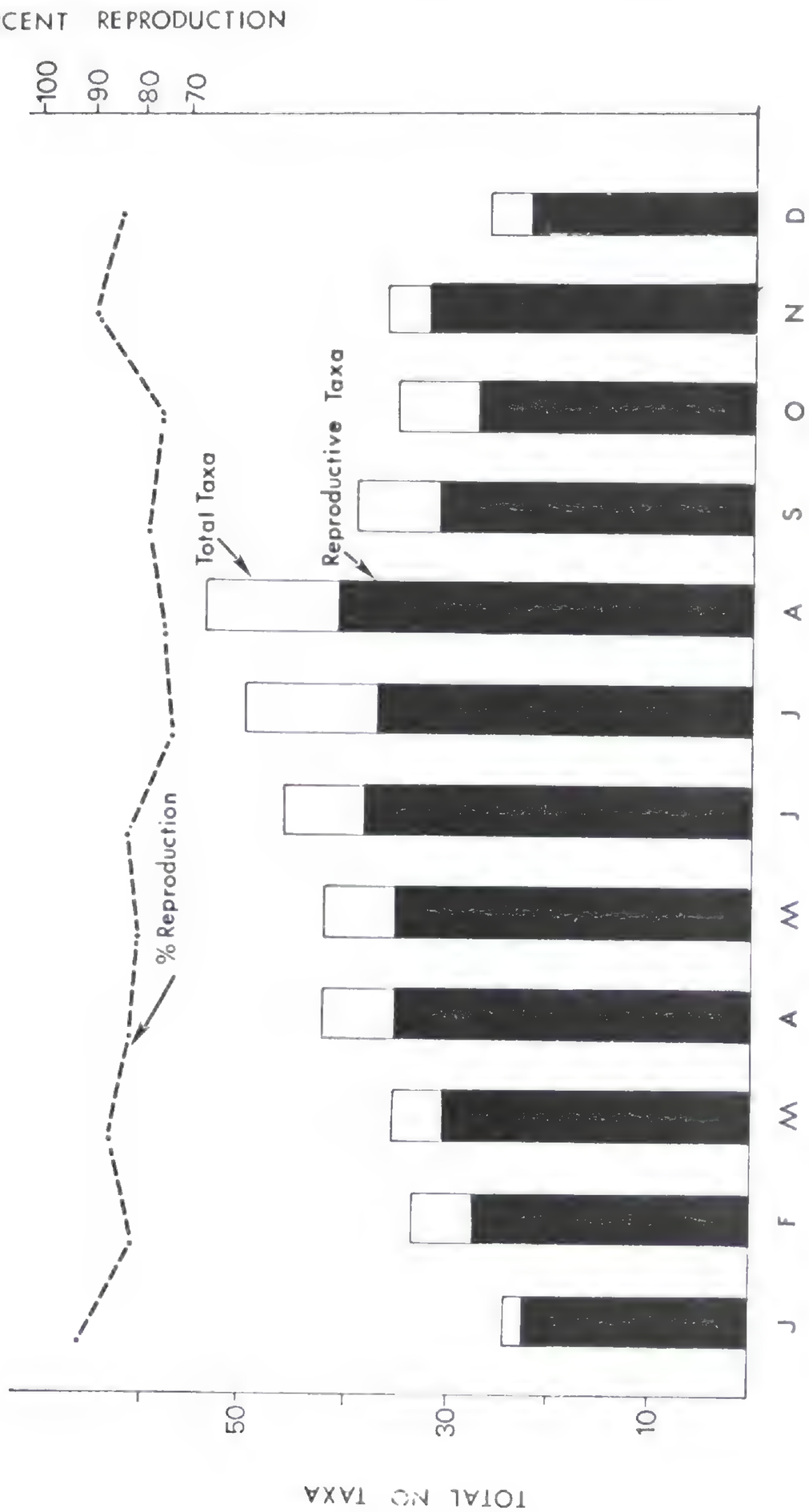

Figure 3. Monthly occurrence and reproduction of phaeophycean taxa in New Hampshire.

Table II. Seasonality, Reproductive Periodicity, Longevity, and Distribution of the Phaecophyceae in New Hampshire*

	Seasonality													
	J	F	M	A	M	J	J	A	S	O	N	D	Longevity	Local Distribution
Agarum cribrosum	U	U	U	U	U	U	U	U	U	U	U	U	Per	1, 2
Alaria esculenta		X	U	U	X	U	U	U	X	U	U	U	Per	1, 2
Ascocyclus distromaticus	P			P	P		P	P	P				A	1, 2
Ascophyllum nodosum	R	R	R	R	R	R	R	R	R	R	R	R	Per	1-4
Ascophyllum nodosum ecad *scorpioides*	R	R	R	R	R	R	X	X	X	X	X	X	Per	3, 4
Asperococcus fistulosus				U		U	U	U	U				A	1, 2
Chorda filum					X	U	U	U	U		U		A	1-4
Chorda tomentosa				X	U	U		U					A	1, 3, 4
Chordaria flagelliformis	U	U	U	U	U	U	U	U	U	U	U	U	A	1-4
Cladostephus spongiosus f. *verticillatus*		X											(?) Per	1
Delamarea attenuata				U	U	U					U		A	1, 4
Desmarestia aculeata	X	U	X	X	X	X	X	X	U	U	X	X	Per	1, 2
Desmarestia viridis	X	X	X	X	X	X	X	X	X				A	1, 2
Desmotrichum undulatum				P	P			P					A	1, 4
Dictyosiphon foeniculaceus			X	X	U	U	U	X	X	X			A	1, 2, 4
Ectocarpus faciculatus							P						A	1
Ectocarpus siliculosus	P	P	P	P	P	PU	P	P	P	P	P	P	A	1-4
Elachista fucicola	U	U	U	U	U	U	U	U	U	U	U	U	Per	1-4
Elachista lubrica							U						(?) Per	1
Eudesme virescens							U						A	1, 2
Fucus distichus ssp. *distichus*	R	R	R	R	R	R	R	R	R	R	R	R	Per	1, 2
Fucus distichus ssp. *edentatus*	R	R	R	R	R	R	R	R	R	R	R	R	Per	1-4
Fucus distichus ssp. *evanescens*	R	R	R	R	R	R	R	R	R	R	R	R	Per	1-4

Fucus spiralis	R	R	R	R	R	R	R	R	R	R	R	R	Per	1, 2, 4
Fucus vesiculosus	R	R	R	R	R	R	R	R	R	R	R	R	Per	1, 2
Fucus vesiculosus var. *spiralis*	R	R	R	R	R	R	R	R	R	R	R	R	Per	3, 4
Giffordia granulosa		P				P	P	P	P	P	P	P	A	1, 3, 4
Giffodia sandriana								P	P				A	4
Giffordia secunda								P					A	2
Hecatonema terminalis													A	
Isthmoplea sphaerophora				U	U	U		U					A	1, 4
Laminaria digitata	U	U	U	U	U	U	U	U	U	U	U	U	Per	1, 2, 4
Laminaria longicruris		X	X	X	X	X	X	X	X	X	X		Per	1, 2, 4
Laminaria saccharina	U	U	U	U	X	X	X	X	U	X	U	U	Per	1-4
Laminariocolax tomentosoides			P	P				P		P		P	(?) A	2
Leathesia difformis				U	U	U	U	U	U	U	U		A	1, 2
Mikrosyphar porphyrae					P		P	P					A	1
Myrionema corunnae		P	P	P	P	P	P	P	P	P	P		A	1, 2, 4
Myrionema magnusii													A	—
Myrionema strangulans						U	U	U					A	1, 2
Petalonia fascia	P	P	P	P	P	P	P	P	P	P	P	P	A	1-4
Petalonia zosterifolia			P	P	P			P			P	P	A	1, 2, 4
Petroderma maculiforme	U	U	U	U	U	U	U	U	U	U	U	U	Per	2, 4
Pilayella littoralis	PU	PU	PU	PU	PU	PU	U	U	U	PU	U	U	A	1-4
Protectocarpus speciosus		P	P	P	P	P	P		P	P	P		(?) A	1, 2
Pseudolithoderma extensum	U	U	U	U	U	U	U	U	U	U	U		P	1, 2, 4
Punctaria latifolia						X	P	P	P	X			A	2, 4
Punctaria plataginea						P	P	P					A	1, 2
Ralfsia bornetii		U	U	UP	U	U		U	U		U		(?) Per	1-4
Ralfsia clavata			U	U		U	U	U	U	U	U	U	(?) Per	2-4
Ralfsia fungiformis		X			X	X	X	X		X			Per	2
Ralfsia verrucosa	U	U	U	U	U	U	U	U	U	U	U	U	Per	1-4

Table II (continued)

	Seasonality													
	J	F	M	A	M	J	J	A	S	O	N	D	Longevity	Local Distribution
Sacchorhiza dermatodea						U	X	X					A	1, 2
Scytosiphon lomentaria var. *lomentaria*	P	P	P	P	P	P	P	P	P	P	P	P	A	1-4
Scytosiphon lomentaria		X	P										A	4
Stictyosiphon griffithsianus								U					Per	2
Ulonema rhizophorum						P							A	4
Sphacelaria cirrosa	U	PU		X		X	X	X	X	X	X	X	Per	1, 2, 4
Sphacelaria fusca							X						(?) Per	1
Sphacelaria plumigera							X	X					Per	2
Sphacelaria plumosa							X	X					(?) Per	2
Sphacelaria racemosa				X			X	X	X				(?) Per	2
Sphacelaria radicans			X		X	X	X	X	X	X	U	X	Per	2, 3
Spongonema tomentosum			P	P	P		P	P		P	P		(?) Per	1, 2
Stictyosiphon griffithsianus					U	U							A	4
Ulonema rhizophorum		P	P	P	P	P	P	P			P		A	1, 2, 4
Total species present by month	24	33	35	42	42	46	50	54	39	35	36	27		

Longevity
A = annual
Per = perennial

Seasonality / Reproductive Structures
P = plurilocular sporangia
R = receptacle
U = unilocular sporangia
X = present

Local Distribution
1 = Isles of Shoals
2 = Nearshore open coast
3 = Hampton-Seabrook Estuary System
4 = Great Bay Estuary System

Estuary System, while only 19 taxa were noted from the Hampton-Seabrook Estuary System. Specific details on the coastal and/or estuarine distributional patterns of each species are given in Table II and in the annotated checklist.

ANNOTATED CHECKLIST

Sixty-six taxa of phaeophycean algae from coastal and estuarine environments within New Hampshire are recorded in the following checklist. Four taxa were rare and only collected once (i.e., *Cladostephus spongiosus* f. *verticillatus*, *Elachista lubrica*, *Giffordia secunda*, and *Sorocarpus micromorus*. Fourteen species are newly recorded. Two of these represent range extensions on the northeastern coast of North America. Thus, *Cladostephus spongiosus* f. *verticillatus* was previously known from New York to southern Massachusetts (Taylor, 1962), while *Protectocarpus speciosus* was earlier recorded from the Canadian Maritime Provinces (South, 1976). Collins (1900) recorded two taxa from the state, namely *Myrionema magnusii* (as *Ascocylus orbicularis*) and *Hecatonema terminalis* (as *Ectocarpus terminalis*), which we have neither collected nor observed as herbarium specimens. Both plants are small epiphytic species, which might have been missed due to their uncommon occurrence.

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* = a range extension on the northeastern coast of North America.
** = a new record for New Hampshire.

PHAEOPHYCEAE

Agarum cribrosum (Mert.) Bory

Common on the open coast, epilithic (0 to −32m), unilocular sporangia recorded each month. Perennial.

Alaria esculenta (L.) Grev.

Common on exposed open coastal sites, epilithic (0 to −18m), unilocular sporangia recorded each season. Perennial.

Ascocyclus distromaticus Taylor

Uncommon, epiphytic on *Palmaria palmata* (0 to −10m) on the open coast. Collected each season, plurilocular reproductive organs observed in each collection. Annual.

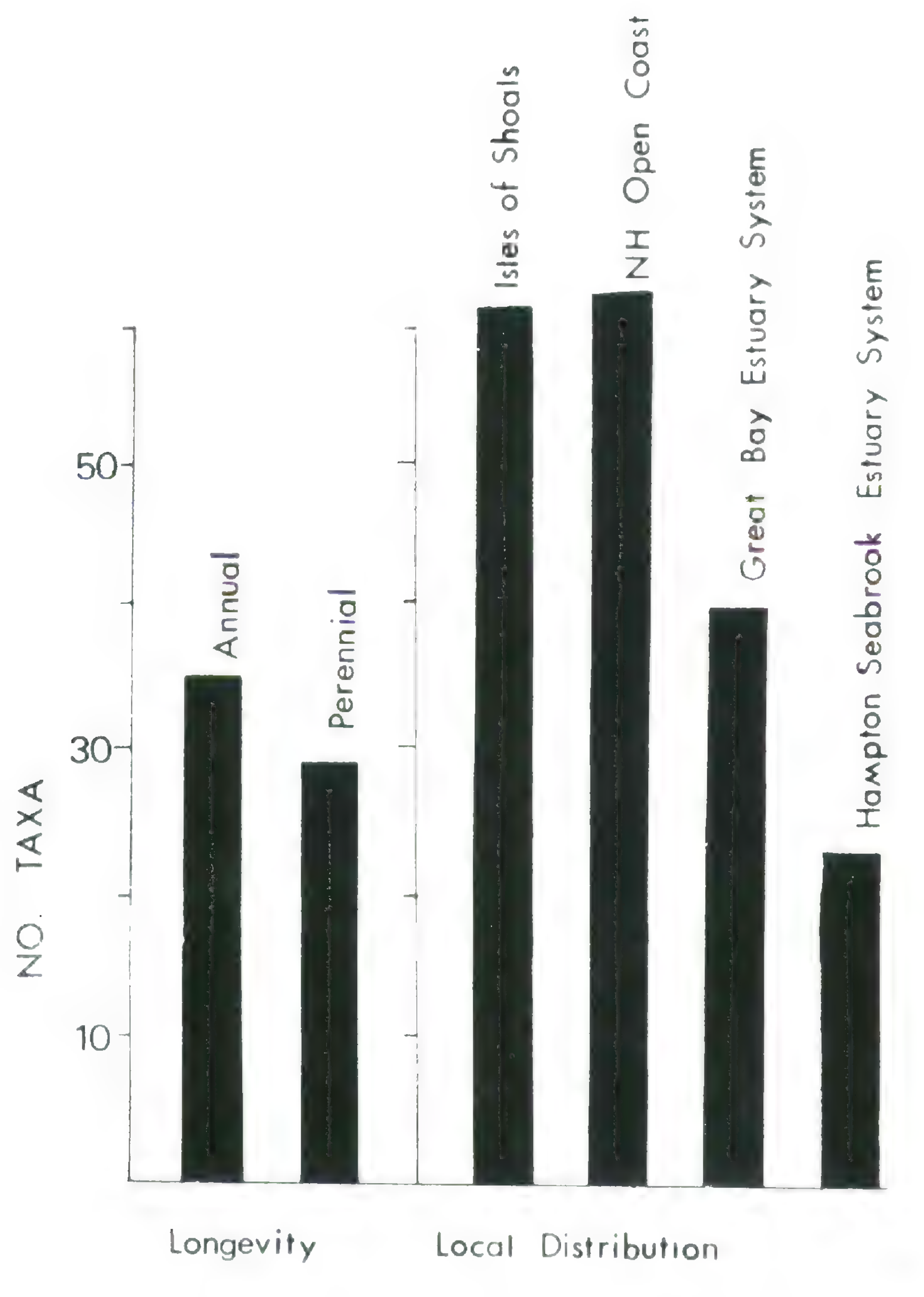

Figure 4. The longevity and local distribution of phaeophycean taxa in New Hampshire.

Ascophyllum nodosum (L.) Le Jol.

Abundant in semi-exposed and sheltered open coastal and estuarine sites, epilithic (0 to +2.0m). Although some reproductive receptacles are present every month, maximum fertility occurs in early spring (Josselyn & Mathieson, 1978, 1980; Mathieson et al., 1976). Perennial.

Ascophyllum nodosum (L.) Le Jol. ecad **scorpioides** (Reinke) Hauck

Occasional as detached plants in estuarine habitats (Chock & Mathieson, 1976, in press); usually entangled amongst the culms of *Spartina alterniflora* (+0.15 to +1.5m). Although fertile receptacles are uncommon they have been recorded from January to June. Perennial.

Asperococcus fistulosis (Huds.) Hook.

Uncommon, on rocks and epiphytic on coarse seaweeds (0 to +0.5m) at the open coast. Collected during the spring and summer, with unilocular sporangia observed in each collection. Annual.

Chorda filum (L.) Stack.

Uncommon on the open coast, rare in estuarine (outer) areas. On rocks (0 to −8m) and collected from May to November, unilocular sporangia observed in each collection, except May. Annual.

Chorda tomentosa Lyngb.

Uncommon, on rocks (0 to −12m) in coastal and estuarine environments; the plant exhibits a broader estuarine distribution than *C. filum*. Collected during April to August, with unilocular sporangia observed betwen May and August. Annual.

Chordaria flagelliformis (O. F. Müll.) C. Ag.

Common on the open coast, less abundant in estuarine habitats. Epilithic and epiphytic (+0.1 to −8.0m). Present throughout the year. Unilocular sporangia recorded every month. Field studies in New England (Mathieson, Hehre, & Reynolds, 1981) and Iceland (Munda, 1979) suggest that forma *densa* Farlow is a juvenile stage of forma *typica*, as young spring specimens have short, dense lateral branches (3–10 mm). Aseasonal annual or biennial (Mathieson et al., loc. cit.).

***Cladostephus spongiosus f. verticillatus** (Lightf.) Lyngb.

Collected once during February. On rocks (+0.1m) at the Isles of Shoals. No reproductive structures observed in the single collection.

Although we have only seen the plant once, it is recorded in an unpublished checklist (Anon., 1975) from the Isles of Shoals. It was previously recorded from New York to southern Massachusetts, as well as being rare north of Cape Cod, (Taylor, 1962). ?Perennial (Sears, 1971).

****Delamarea attenuata** (Kjell.) Rosenv.

Uncommon, on rocks (+1.0 to +1.5m) at the Isles of Shoals and with a single estuarine collection near the mouth of the Piscataqua River. Found during April to November, with unilocular sporangia in each collection. Annual.

Desmarestia aculeata (L.) Lamour.

A common epilithic species (0 to −26m) on the open coast. Unilocular sporangia observed in February, September, and October. Perennial.

Desmarestia viridis (O. F. Müll.) Lamour.

Common, on rocks within low tide pools and the sublittoral zone (+0.2 to −20m) of the open coast. Collected from January to September. Annual.

Desmotrichum undulatum (J. Ag.) Reinke

Uncommon, on *Chaetomorpha aerea* and *Cladophora sericea* in tide pools (+1.0 to +2.5m) at the Isles of Shoals, also on *Zostera marina* at a few estuarine habitats (0 to −3.0m). Collected during spring and summer, with plurilocular reproductive organs in each collection. Annual.

Dictyosiphon foeniculaceus (Huds.) Grev.

Common on rocks or epiphytic on *Chordaria flagelliformis*. Present within or outside tide pools in the lower eulittoral (+0.1m), also extending to the sublittoral zone (−12m). Primarily found on the open coast, but with a few collections from outer estuarine sites —e.g., Piscataqua River. Collected from March to October, with unilocular sporangia observed during May to July. Collins (1900) and Croasdale (1941) record the forma *hippuroides* and variety *hispidus*. Our observations, as well as those of Jaasund (1965), suggest that the plant's morphology encompasses the short-branched variety *hispidus* and the exposed open-coastal forma *hippuroides*. Annual.

Ectocarpus fasciculatus Harvey

Collected once (July) at the Isles of Shoals (Star Island), epiphytic on *Laminaria* (Croasdale, 1941) and with plurilocular reproductive organs. Annual.

Ectocarpus siliculosis (Dillw.) Lyng.

Common on rocks and epiphytic (+0.3 to −20m). Found with plurilocular reproductive organs throughout most of the year. Unilocular sporangia observed in June. Aseasonal annual.

Elachista fucicola (Vell.) Aresch.

Common, epiphytic on *Ascophyllum nodosum,* occasionally on *Fucus* sp. Most abundant at the open coast, but with several estuarine records. Present with unilocular sporangia throughout the year. Perennial.

Elachista lubrica Rup.

Collected once (July) with unilocular sporangia, at the Isles of Shoals (Star Island), epiphytic on *Fucus* sp. (Croasdale, 1941). The species is also recorded in an unpublished checklist (Anon., 1975) from the Isles of Shoals. Perennial (?).

Eudesme virescens (Carm. *ex* Harv. in Hook.) J. Agardh

Collected twice in mid-summer (July), on rocks (+0.1 to −3.0m) from the open coast; unilocular sporangia observed in both collections. Summer annual.

Fucus distichus L. ssp. **distichus** L. emend. Powell

A common open coastal species, on rocks within high eulittoral tide pools (+2.0 to +3.5m); receptacles present throughout the year, but uncommon during June to August. Perennial.

Fucus distichus L. ssp. **edentatus** (DLP) Powell

Common on rocks at the open coast and with a few outer estuarine collections (+0.5 to −9.0m). Receptacles present throughout the year; however, major peaks of reproduction occur in the spring and late summer (E. Sideman, personal communication). The plant is often difficult to distinguish from *F. distichus* ssp. *evanescens,* particularly in the spring and in estuarine locales. Perennial.

Fucus distichus L. ssp. **evanescens** (C. Ag.) Powell

Common in estuarine habitats, less abundant on the open coast, where it is primarily found in semi-exposed to sheltered locations. Growing on rocks (+0.5 to −9.0m). Although receptacles are found throughout the year, reproduction is distinctly maximal in the spring at estuarine areas versus the spring and late summer at open coastal sites (E. Sideman, personal communication). The plant is often difficult to distinguish from *F. distichus* ssp. *edentatus* particularly when it is reproductively immature. Perennial.

Fucus spiralis L.

Common on the open coast, and with scattered estuarine populations. On rocks (+2.0 to +3.0m), often forming a distinct belt above *A. nodosum* and *F. vesiculosus.* Although receptacles are found throughout the year, the plant exhibits a pronounced summer reproductive maximum (Niemeck & Mathieson, 1976). Perennial.

Fucus vesiculosus L.

An ubiquitous epilithic plant on the open coast, occasionally epiphytic on *A. nodosum* (+0.25 to +2.5m). The species is replaced within estuarine habitats by var. *spiralis* Farlow. Although fertile receptacles are found throughout the year, their maximum numbers occur during the spring (Mathieson et al., 1976). Perennial.

Fucus vesiculosus L. var. **spiralis** Farl.

A common estuarine plant, on small rocks and shingle (+1.0 to +2.0m). Occasionally found detached and entangled amongst the culms of *Spartina alterniflora.* Receptacles are present throughout the year, but exhibit a pronounced maximum during the spring (Mathieson et al., 1976). Perennial.

Giffordia granulosa (Smith) Hamel

Found occasionally in estuarine habitats and once at the open coast, epiphytic and epilithic (+0.3 to −3.0m). Collected during February and June to December; with plurilocular reproductive organs in each collection. Annual.

****Giffordia sandriana** (Zanard.) Hamel

Found twice (August and September) on rocks at a single estuarine site (−1.0 to −2.0m), plurilocular reproductive organs in both collections. Annual.

Giffordia secunda (Kütz.) Batters

Collected once (August), on rocks (−2.0m) at the open coast; with dimorphic plurilocular reproductive organs. Annual.

Hecatonema terminalis (Kütz) Kylin

Recorded by Collins (1900) from New Hampshire (as *Ectocarpus terminalis*), with no specific date nor collecting site. Annual.

****Isthmoplea sphaerophora** (Carm. *ex* Harv. in Hook.) Kjellman

Uncommon, epizoic on sertularians, as well as epiphytic on various coarse seaweeds (+0.2 to −3.0m). Collected during spring and summer; unilocular sporangia observed in each collection. Annual.

Laminaria digitata (Huds.) Lamour.

Common on rocks at the open coast (+0.1 to −18m), and with scattered estuarine populations in strong tidal rapid sites (Mathieson et al., 1977). Unilocular sporangia present year round but most abundant during the winter. Perennial.

Laminaria longicruris DLP

Occasional, on rocks (0 to −26.0m) in open coastal and estuarine habitats. No reproductive specimens observed. Perennial.

Laminaria saccharina (L.) Lamour.

Common in sublittoral habitats (0 to −26.0m) containing solid substratum. The taxon is more abundant than *L. digitata* in sheltered open coastal and estuarine habitats. Unilocular sporangia observed during each season but most abundant during the winter. Perennial.

Laminariocolax tomentosoides (Farl.) Kylin

Occasional, epiphyte of *Laminaria* spp. on the open coast. Found during March to December, with plurilocular reproductive organs observed in each collection. Annual (?).

Leathesia difformis (L.) Aresch.

Present from April to November at the open coast; most common during the summer. On rocks and various algae (+0.5 to −6.0m). Unilocular sporangia observed in each collection. Annual.

****Mikrosyphar porphyrae** Kuck.

Uncommon, endophytic within *Porphyra* spp. at the Isles of Shoals (+2.5 to −3.0m). Collected during May to August, with plurilocular reproductive organs in each collection. Annual.

****Myrionema corunnae** Sauv.

Common, on *Laminaria* spp. (0 to −11m) at the open coast and with a single estuarine record. Collected from February to November, with plurilocular reproductive organs in each collection. Annual.

Myrionema magnusii (Sauv.) Loiseaux

Recorded by Collins (1900) from New Hampshire (as *Ascocylus orbicularis*), with no specific date nor collecting site. Annual.

Myrionema strangulans Grev.

Occasional, epiphytic on various seaweeds (+0.5 to −5.0m), particularly *Ulva lactuca*. Collected from June to August; primarily found on the open coast, but with a single estuarine record. Unilocular sporangia observed in each collection. Annual.

Petalonia fascia (O. F. Müll.) Kuntze

Common, epilithic and epiphytic from the upper eulittoral (in tide pools) to the sublittoral fringe zones (+2.3 to −0.1m). Present with plurilocular reproductive organs throughout the year, but most prevalent during the winter and spring. The plant alternates with *Ralfsia hornetii* and *R. clavata* (Edelstein, et al., 1970). Annual.

****Petalonia zosterifolia** (Reinke) O. Kuntze

Uncommon, on rocks (+0.2 to 0.0m), primarily at the open coast —but with a few estuarine collections. Found during March December, and with plurilocular reproductive organs in each collection. Annual.

****Petroderma maculiforme** (Wollny) Kuck.

Common on rocks at several estuarine sites, less abundant at the open coast (0 to −8.0m). Present throughout the year, with unilocular sporangia observed in each collection. It is tolerant of consistently low, as well as fluctuating salinities. As noted by Wilce, et al. (1970), the taxon has a broad boreal-arctic distribution, extending from southern Massachusetts to the high arctic, northwest Greenland, and eastern Canadian archipelago. Perennial.

Pilayella littoralis (L.) Kjell.

Common, found throughout the year but most prevalent during the spring and early summer (Chock & Mathieson, in press). On rocks and epiphytic on coarse seaweeds (0 to +1.5m) in a wide

variety of coastal and estuarine habitats, extremely tolerant of salinity fluctuations. Unilocular sporangia recorded each month; plurilocular reproductive organs seen during January to June and October. Aseasonal annual.

***Protectocarpus speciosus** (Borg.) Kuck.

Occasional, epiphytic on *Chaetomorpha aerea* at the open coast (+0.1 to +1.5m). Collected during July to November, with plurilocular reproductive organs observed in each collection. Annual (?).

Pseudolithoderma extensum (Crouan frat.) S. Lund

A common crustose species, epilithic at numerous coastal and estuarine locations (0 to −8.0m). Collected with unilocular sporangia each month. Perennial.

Punctaria latifolia Grev.

Uncommon, epiphytic on *Zostera marina* and several seaweeds (0 to −3m) in estuarine and open coastal areas. Collected during June to October, with plurilocular reproductive organs observed from July to September. Annual.

Punctaria plantaginea (Roth) Grev.

Uncommon, collected between June and August on the open coast, epilithic (+0.1 to −3.0m). Plurilocular reproductive organs observed in each collection. Annual.

Ralfsia bornetii Kuck.

Occasional, growing on rocks (+1.5 to −11.0m) on the open coast and occasionally in estuarine habitats. Found throughout most of the year, unilocular sporangia in all collections, plurilocular reproductive organs seen only in April. As noted by Edelstein, et al. (1970) the plant is part of the life history of *Petalonia fascia.* Perennial (?).

Ralfsia clavata (Harv. in Hook.) Crouan frat.

Occasional, epilithic (+1.0 to −26.0m) at open coastal and estuarine areas. Observed during March to December with unilocular sporangia in all collections. As described by Edelstein, et al. (1970) it may be part of the life history of *Petalonia fascia.* Perennial (?).

Ralfsia fungiformis (Gunn.) Setch. *et* Gard.

Occasional, collected all seasons, on rocks (0 to −8m) at the open coast; no sporangia observed. Perennial.

Ralfsia verrucosa (Aresch.) J. Agardh

Common on rocks within the upper eulittoral (in tide pools) to the sublittoral zone (+2.2 to −26m) at a wide variety of coastal and estuarine sites. Unilocular sporangia observed each month. Perennial.

Saccorhiza dermatodea (DLP) J. Ag.

Uncommon, attached to rocks within the sublittoral zone (0 to −15m) on the open coast. Collected from June to August, with unilocular sporangia observed in June. Annual.

Scytosiphon lomentaria (Lyngb.) Link var. **lomentaria**

Common on rocks, occasionally epiphytic on coarse seaweeds (0 to +2.7m). Present with plurilocular reproductive organs throughout the year, but most prevalent during the winter and spring. Annual.

****Scytosiphon lomentaria** (Lyngb.) Link var. **complanatus** Rosenv.

Locally abundant at one estuarine site during February and March, on rocks (0 to −3m). Plurilocular reproductive organs observed in March. Clayton (1980) gives a detailed account of the complanate and cylindrical plants of *S. lomentaria*. She emphasizes that the two are distinct, although the taxonomic significance of their differences still requires further investigation. Annual.

Sorapion kjellmanii (Wille) Rosenv.

Recorded once (August) with unilocular sporangia; found on small rocks within the sublittoral zone (−6m) of a sandy open coastal site. Perennial.

****Sorocarpus micromorus** (Bory) Silva

Found once (June) with plurilocular reproductive organs, growing on rocks within the lower eulittoral zone (+0.1m) at an estuarine site. Annual.

Sphacelaria cirrosa (Roth) C. Ag.

Common on the open coast, less abundant in estuarine habitats, forming small tufts on vertical rock faces (+0.2 to +1.4m) and extending to −11.0m. It is often found under *Ascophyllum nodosum* and *Fucus vesiculosus* and occasionally as an epiphyte on both species. Present throughout the year, with plurilocular reproductive

organs observed in February, unilocular sporangia in January and February, propagules in June, July, September, and October. Perennial.

****Sphacelaria fusca** (Huds.) C. Ag.

Found once (July) at the Isles of Shoals on rocks within the lower eulittoral zone (0.1m). Biradiate propagules observed but no other reproductive structures. According to De Haas-Niekerk (1965) *S. fusca* equals *S. furcigera*. Perennial (?).

****Sphacelaria plumigera** Holmes

Recorded twice (July and August) on rocks (0 to −12m) from the open coast. Perennial.

Sphacelaria plumosa Lyngb.

Uncommon, collected during July and August on rocks (0 to −18m) at the open coast. Perennial (?).

Sphacelaria racemosa Grev.

Locally abundant on rocks within the sublittoral zone (0 to −18m) at the open coast. Collected during April and July to September. As suggested by Sears (1971) the plant is distinct from *S. arctica* (= *S. racemosa* var. *arctica* in Taylor, 1962). Perennial (?).

Sphacelaria radicans (Dill.) C. Ag.

Locally common on rocks (+0.1 to −12.0m) in sandy open coastal sites (Daly & Mathieson, 1977) and with a single outer estuarine collection. Collected during all seasons, unilocular sporangia present in November. Perennial.

Spongonema tomentosum (Huds.) Kutz.

Uncommon, epiphytic on fucoid and other coarse algae (+0.2 to +0.5m) from the open coast. Collected during March to November with plurilocular reproductive organs in all but the March collection. Perennial (?).

****Stictyosiphon griffithsianus** (Le Jol.) Holmes *et* Batt.

Rare, collected three times during May and June at two estuarine locations. Epiphytic on *Palmaria palmata* within the upper sublittoral zone (0 to −3m) with unilocular sporangia observed in each collection. Annual.

Ulonema rhizophorum Foslie

A common epiphyte on *Dumontia contorta* (Kilar & Mathieson, 1978); seen from February to August and November with plurilocular reproductive organs observed in all collections. Annual.

DISCUSSION

The brown algal flora of New Hampshire exhibits a pronounced seasonal cycle (Figure 3) with the highest number of species in the summer and the lowest numbers in the winter. In contrast, the Phaeophyceae in more southerly areas like Florida usually show a winter or early spring maximum and a summer minimum (Earle, 1969, 1972; Mathieson & Dawes, 1975). Coleman and Mathieson (1975) suggest that the geographical differences in seasonal succession may be due to varying thermal regimes and amplitudes. Chapman (1964) and Williams (1948, 1949) also emphasize that seasonally dynamic floras and a wide range of annuals exist in areas with pronounced temperature fluctuations. The functional role of annuals in mediating the seasonal cycle of brown algae in New Hampshire is shown in Table II as there are two major groups of annuals: (1) aseasonal annuals that reproduce throughout the year and that are represented by successive populations, and; (2) seasonal annuals. Hehre and Mathieson (1970) have recorded similar characterizations of the marine rhodophycean annuals in New Hampshire.

A synthesis of the reproductive information in Table II (i.e. all 66 taxa) shows that the levels are highest in late fall-winter and lowest in the summer (Fig. 3). Similar patterns have been described by several other investigators (Scagel, 1966; Russell, 1973). Interestingly there was an apparent inverse relationship between total reproduction and species diversity (Fig. 3).

As might be expected, the greatest diversity of brown algae were found on the open coast of New Hampshire, with reduced numbers of species in estuarine habitats (Fig. 4). Other investigators (Doty & Newhouse, 1954; Mathieson & Fralick, 1972; Mathieson, Reynolds, & Hehre, 1981), have noted a similar estuarine reduction pattern which probably results from a lack of stable substratum and variable salinity, as well as temperature conditions. In turn, the greater diversity of brown algae within the Great Bay as compared to the Hampton-Seabrook Estuary Systems is probably due to its greater size, number of habitats, and availability of substrata (see Mathieson, Reynolds, & Hehre, 1981; Reynolds & Mathieson, 1975).

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DEPARTMENT OF BOTANY AND PLANT PATHOLOGY
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STUDIES ON *MENTHA* × *DUMETORUM* SCHULT. (LABIATAE) TO CONFIRM ITS PRESUMED PARENTAGE — *M. AQUATICA* LINN. × *M. LONGIFOLIA* (LINN.) HUDS.

B. O. B. FAGBEMI[1] AND J. K. MORTON

ABSTRACT

A study of synthesized hybrids and wild strains of the species of *Mentha* has confirmed the origin and parentage of *M.* × *dumetorum* Schultes, (*M. aquatica* × *M. longifolia*). The study was based on morphology, chromosome number, meiotic behaviour, and pollen and seed fertility.

Chromosome numbers of $2n = 60$, 72, were obtained for *M.* × *dumetorum*. The interspecific hybrids showed 100% sterility correlated with meiotic irregularities.

Mentha is one of the larger and taxonomically more complex genera of the Labiatae. Briquet (1897) recognised only 15 species in the genus. Most of these species are involved in the formation of hybrids, which accounts in large measure for the extensive variation and taxonomic complexities in the genus.

Though there is considerable literature on hybrids in the genus *Mentha*, that with a bearing on the origin of *Mentha* × *dumetorum* is sparse. The object of this paper was to compare several wild strains of this hybrid with synthesized strains of known parentage using morphology, chromosome number, meiotic behaviour, and pollen and seed fertility in order to understand and confirm the origin of *M.* × *dumetorum*.

Mentha × *dumetorum* is believed to be a hybrid between *M. aquatica* L. ($2n = 96$) and *M. longifolia* L. ($2n = 24$ and 48) and is intermediate in morphology and chromosome number between the two species. These species have also been studied for comparative purposes. Schultes (1809) was the first to describe this hybrid and considered it to be intermediate between *M.* × *nemorosa* Willd. (i.e. *M.* × *villosa* Huds.) and *M. sylvestris* L. (i.e. *M. longifolia*). A fuller description of this hybrid is also given in Clapham, Tutin, and Warburg (1960).

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MATERIALS AND METHODS

The plant materials used were collected in the wild in Britain and North America by Professor J. K. Morton, and also obtained from various botanical gardens. The artificially produced hybrid strains were synthesized by Dr. M. J. Murray (A. M. Todd Company, Kalamazoo, Michigan, U.S.A.), who crossed a male-sterile strain of *M. aquatica* with fertile diploid and tetraploid strains of *M. longifolia*. Table I gives the list of the plant materials investigated.

The plants were brought into cultivation by transplanting the rhizomes or by growing from seeds. During winter they were grown in pots in the green houses to protect them from the severity of the climate at Waterloo, Ontario, Canada. In summer they were grown outside in the experimental garden under relatively uniform conditions.

Chromosome counts were made from root-tip preparations using standard acetocarmine technique. Young flower buds were used to study meiotic behaviour and the development of the pollen. The flower buds were fixed for 12 to 36 hours in either Carnoy's fluid (6 parts absolute alcohol, 3 parts chloroform, and 1 part glacial acetic acid), or in 1:3 acetic-alcohol to which ferric acetate had been added to intensify staining. They were then transferred to 70% alcohol, in which they could be stored for several days. The anthers were subsequently squashed in 2% acetocarmine. Slides were made permanent using McClintock's method (in Johansen, 1940). "Euparal" was used as the mountant.

Pollen fertility was determined by staining the pollen grains with standard glycero-acetocarmine, prepared by mixing equal volumes of 50% glycerine and 2% acetocarmine.

The well stained and well formed grains were considered to be fertile, while those which were small, malformed, or shrivelled and unstained were regarded as aborted.

RESULTS

At the outset of this study we had living material of 13 strains of mints which were believed to be referable to *Mentha* × *dumetorum*. Seven were of natural origin, collected in the wild or obtained from garden sources, whilst the others were synthesized hybrids produced by Dr. Murray. In addition we had a range of herbarium material of

TABLE I. **List of Mentha Material Examined and their Chromosome Numbers**[1]

TAXON	ORIGIN	ACCESSION NO	2*n*
Species: —			
M. aquatica	Paris, B.G. (Native)	—	96
M. longifolia	Newmill, Penzance, U.K.	JKM 219	24
M. longifolia	Cambden, Maine, U.S.A. (Cultivated)	M 31	48
Hybrids: —			
M. × *dumetorum*	Leiden, B.G.	M 26 (= M 58)	72
M. × *dumetorum*	England (without precise locality)	M 72	72
M. × *dumetorum*	Dijon, B. G.	M 77	72
M. × *dumetorum*	Newmill, Penzance, U.K.	JKM 5218	72
M. × *dumetorum*	St. Just., Cornwall, U.K.	JKM 5201	72
M. × *dumetorum*	Synthesized	M 71	60
M. × *dumetorum*	Synthesized	M 73	72
M. × *dumetorum*	Synthesized	M 74	72
M. × *dumetorum*	Synthesized	M 87	60
M. × *dumetorum*	Synthesized	M 88	72
M. × *dumetorum*	Synthesized	M 90	C 84
M. × *Piperita*	Nova Scotia	NA 4264	72

[1]Voucher specimens deposited at the Biology Department, University of Waterloo, Ontario Canada.

this hybrid, its presumed parent species, and other similar hybrids. These were used in the study of the morphology.

The initial study carried out on *M.* × *dumetorum* was of its morphological characteristics. In particular it was necessary to define and identify *M.* × *dumetorum*, for it is not always readily separable from other mints, especially hairy forms of *M.* × *piperita* (*M. aquatica* × *M. spicata*).

The measurable characters used in determining materials of wild origin are the length of calyx, leaf index, inflorescence breadth, and the leaf base form. Table II gives summary of data for recorded characters in the natural and synthesized strains of *Mentha* × *dumetorum*, the pubescent forms of *M.* × *piperita*, and in the two parent species of *M.* ×*dumetorum* — *M. longifolia* and *M. aquatica*.

Leaf size, leaf shape, inflorescence structure, and other salient characters do not differ significantly between the "wild" and synthesized hybrids. The hybrids were typically intermediate with

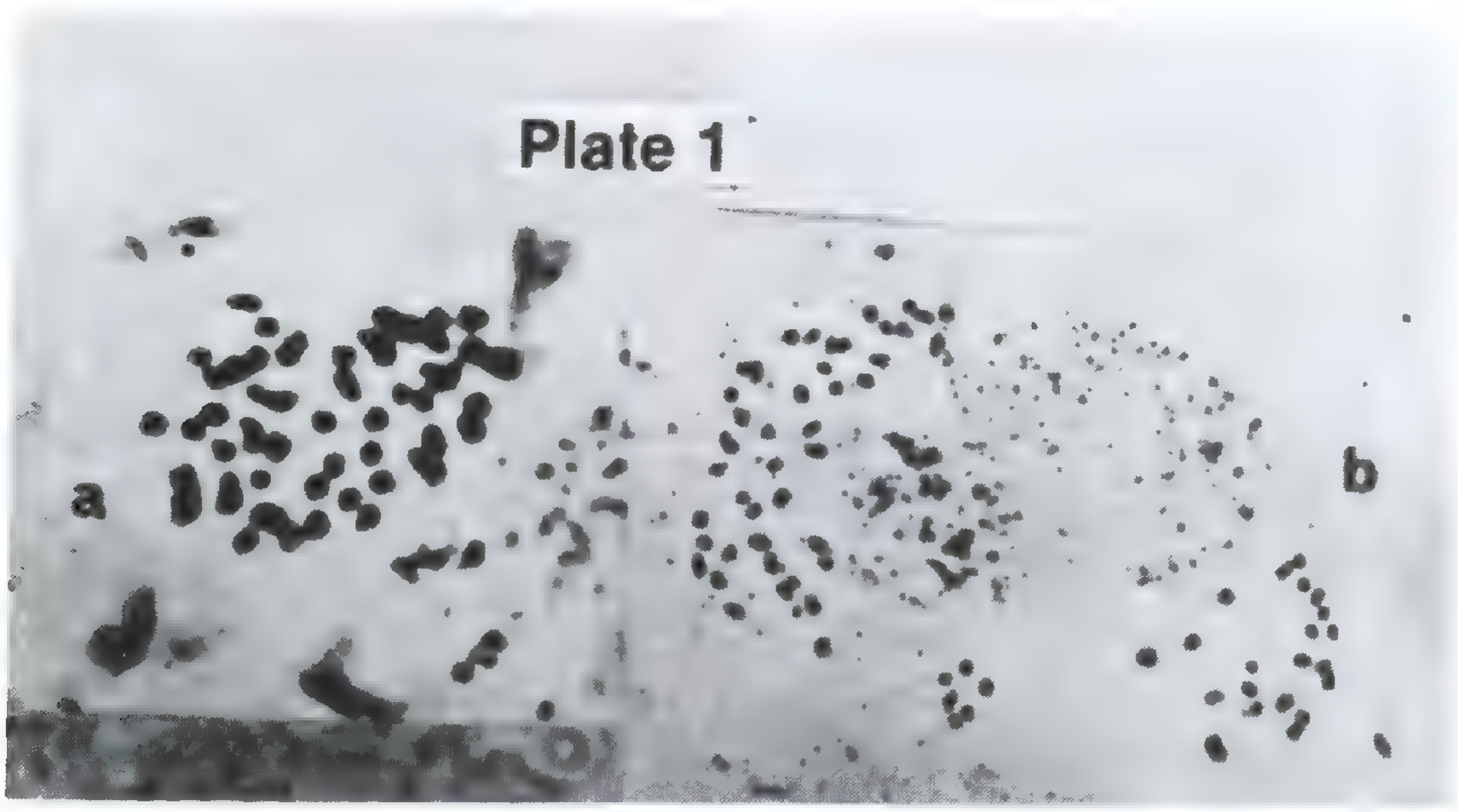
respect to the salient features of their parents, although they showed some variation in such characters as the size of leaves, and in the degree of pubescence on the leaf and stem. Thus a comparison of the artificial hybrids with those of natural occurrence showed them to be similar, and intermediate in morphological appearance between their parental species.

TABLE II. **Characters in Mentha × dumetorum, M. × Piperita and two parents of M. × dumetorum — M. longifolia and M. aquatica**

Taxon	Accession No.	2*n*	Calyx (mm)	Leaf (cm) L × B	Leaf Index L ÷ B	Inflor. Breadth (cm)	Leaf Base
M. × *dumetorum*	M26 = (58)	72	2.5	3.2 × 1.7	1.9	1.0	cuneate
M. × *dumetorum*	M72	72	2.9	4.4 × 2.3	1.9	1.4	round
M. × *dumetorum*	M77	72	2.5	5.7 × 3.2	1.8	1.6	round
M. × *dumetorum*	JKM 4583	72	2.5	5.1 × 3.0	1.8	1.4	round
M. × *dumetorum*	JKM 5201	72	2.3	4.5 × 3.0	1.6	1.4	round
M. × *dumetorum*	JKM 5202	72	2.3	4.4 × 2.8	1.6	1.4	round
M. × *dumetorum*	JKM 5218	72	2.4	5.1 × 3.4	1.6	1.4	round
M. × *dumetorum*	M71	60	2.0	3.1 × 1.4	2.2	1.4	round
M. × *dumetorum*	M73	72	2.3	4.9 × 2.7	1.8	1.2	round
M. × *dumetorum*	M74	72	2.5	4.5 × 2.5	1.9	1.4	round
M. × *dumetorum*	M87	60	2.5	3.7 × 1.9	2.0	1.4	round
M. × *dumetorum*	M88	72	2.3	5.0 × 2.6	1.9	1.5	round
M. × *dumetorum*	M90	84	2.8	5.7 × 3.0	2.0	1.5	round
M. longifolia	M31	48	1.5	5.1 × 2.0	2.6	0.6	cordate
M. longifolia	JKM 4875	48	2.1	5.5 × 2.5	2.2	1.0	cordate
M. longifolia	JKM 5219	24	2.1	5.5 × 2.1	2.6	1.1	Sub-cordate
M. aquatica		96	3.6	3.5 × 2.0	1.8	1.0	cuneate
M. aquatica	JKM 4879	96	3.6	3.4 × 2.5	1.4	1.7	cuneate
M. aquatica	JKM 4889	96	3.5	4.9 × 3.6	1.4	2.0	cuneate
M. aquatica	NA 44264	72	3.3	8 × 3.5	1.3	1.3	cuneate
M. × *Piperita*	RAG 13	72	3.4	7.8 × 3.3	2.4	1.2	cuneate

The chromosome numbers of 12 strains of *Mentha* × *dumetorum* studied in the present work are $2n = 60$ and 72 (Table I, Plate 1).

Plate 1 (a) *M.* × *dumetorum* M87, $2n = 60$
(b) *M.* × *dumetorum* M77, $2n = 72$



Studies on meiosis during pollen mother cell formation in *M.* × *dumetorum* indicate irregular meiotic behaviour in 7 of the hybrids examined and complete premeiotic abortion in the remaining 5 strains. All the plants which we examined in which meiosis took place had mainly bivalents and univalents with only a few multivalents. In several cases lagging chromosomes and bridges were observed, and these frequently led to the formation of micronuclei. The formation of unequal tetrads frequently occurred, along with triads, dyads, and occasional monads.

Meiotic chromosome numbers were confirmed for *Mentha aquatica* ($n = 18$) and *M. longifolia* ($n = 12$) with normal meiosis and pollen formation (see Fedorov, An.A., 1969, p366).

All strains of *Mentha* × *dumetorum* examined in this study were sterile and produced no fertile pollen. No seed was set in any of the material grown in the garden which was subject to open pollination.

DISCUSSION

In the hybrid, *Mentha* × *dumetorum,* most morphological characters are found to be intermediate, but values of certain characters were often found to be close to those of one of the parents. Considerable differences in the size of leaves and calyx were observed within the hybrids. It was also noted that hybrid strains in *M.* × *dumetorum* in which there were two or more somatic chromosome numbers (as exemplified by natural material from Leiden, (M26) with $2n = 72$ and M71, synthesized, with $2n = 60$) were morphologi-

cally very difficult to distinguish from one another. These factors make it difficult to predict the origin and parentage of any hybrid on the basis of morphology only, without determining chromosome number. The value of chromosome numbers, as pointed out by Davis and Heywood (1963), is that they often show a high degree of stability.

In *Mentha* × *dumetorum* the chromosomes are small and similar in appearance so that their morphology does not provide a useful character. However, *M.* × *dumetorum* species form a polyploid series so that comparisons of chromosome numbers are useful in determining the parentage of many of the hybrids. In all cases the synthesized hybrids proved to have the chromosome numbers to be expected from their known parentage, these numbers being intermediate between those of the parent species. Thus *M.* × *dumetorum* synthesized by crossing *M. aquatica* ($2n = 96$) with either diploid or tetraploid *M. longifolia* ($2n = 24$ and 48), chromosome numbers of $2n = 60$ and 72 were obtained (Table I). These numbers were also obtained in morphologically similar material of *M.* × *dumetorum* from wild sources.

In *Mentha* × *dumetorum* different chromosome numbers in the parental species involved in the formation of hybrids resulted in irregular meiotic behaviour. This was similar in both the synthesized hybrids and those of wild origin in which meiosis occurred. The occurrence of complete or near complete bivalent formation was observed in all the species, whilst the hybrids showed irregular chromosome asociations — univalents, bivalents, and multivalents — at diakinesis and at metaphase I.

The interspecific hybrids in *Mentha* × *dumetorum* showed 100% sterility, correlated with meiotic irregularities. Snyder (1951) made similar observations on *Elymus* hybrids and associated the cause of sterility with gross meiotic irregularities.

CONCLUSION

A comparison of synthesized hybrids with ones of natural origin on the basis of morphology, chromosome number, meiotic behaviour, and fertility has confirmed the parentage of *Mentha* × *dumetorum* Schultes to be *M. aquatica* × *M. longifolia*.

The following chromosome numbers were obtained for *M. dumetorum* ($2n = 60,72$).

The high pollen sterility recorded for *Mentha* × *dumetorum* in both naturally occurring and synthesized hybrids was correlated with meiotic irregularities. None of the 13 strains of *M.* × *dumetorum* produced any pollen or seed.

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A NOTE ON THE OCCURRENCE OF ROOT-SHOOTS IN *VACCINIUM CORYMBOSUM* L.

S. P. VANDER KLOET

Shoots arising from woody rhizomes in the lowbush blueberries in *Vaccinium* § *Cyanoccocus* A. Gray are a well established fact (see, for example, Harshberger, 1916; Camp 1945; Eaton 1949; and Hall 1957). However the crown-forming highbush blueberry, *V. corymbosum* L., except for a few hexaploids (2n = 6x = 72) in the Florida Panhandle and on isolated mountain peaks in North Carolina and Tennessee and tetraploids (2n = 4x = 48) in eastern Quebec where this species introgresses with *V. angustifolium* Aiton (Vander Kloet 1980), rarely produces rhizomes and it has been argued that dispersion in *V. corymbosum* is strictly through the establishment of seedlings.

Thus when I was botanizing a *Gordonia* bayhead on the Archbold Biological Station, 10 km S of Lake Placid, Highlands County, Florida on 27.11.78 and saw several small *V. corymbosum* plants (Figure 1) growing 2–3(5) m away from several large shrubs, I presumed them to be seedlings. However on excavating several of these "seedlings", I found that the "taproot" joined a lateral "rhizome" which meandered through the litter at a depth of 2–5 cm (Figure 1). These laterals could easily be traced back to the large shrubs 2–3 m away.

Cross sections of this "rhizome" (figure 2) showed no pith cells and confirmed my suspicion that indeed these were root-shoots. Furthermore, when I compared this cross section with those published by Hall (1957) I found that mine closely matched his cross section of the *V. myrtilloides* Michx tap root, but not the rhizome of *V. angustifolium*.

This is the first time that a root-shoot has been reported for *Vaccinium* § *Cyanococcus* but their frequency of occurrence is still imperfectly known. So far I have observed them only on diploid plants of *V. corymbosum* in Florida and Texas.

Root-shoots however are not entirely unknown in the angiosperms and have been reported for *Cirsium arvense* (L.) Scop., *Robinia pseudoacacia* L., and *Populus alba* L., inter alia. Moreover their occurrence in *V. corymbosum* certainly complicates our concept of the species' reproductive strategy.

Figure 1. Root-shoot of *Vaccinium corymbosum* L. Voucher at ACAD, *Vander Kloet 1271178*. Magnified two times.

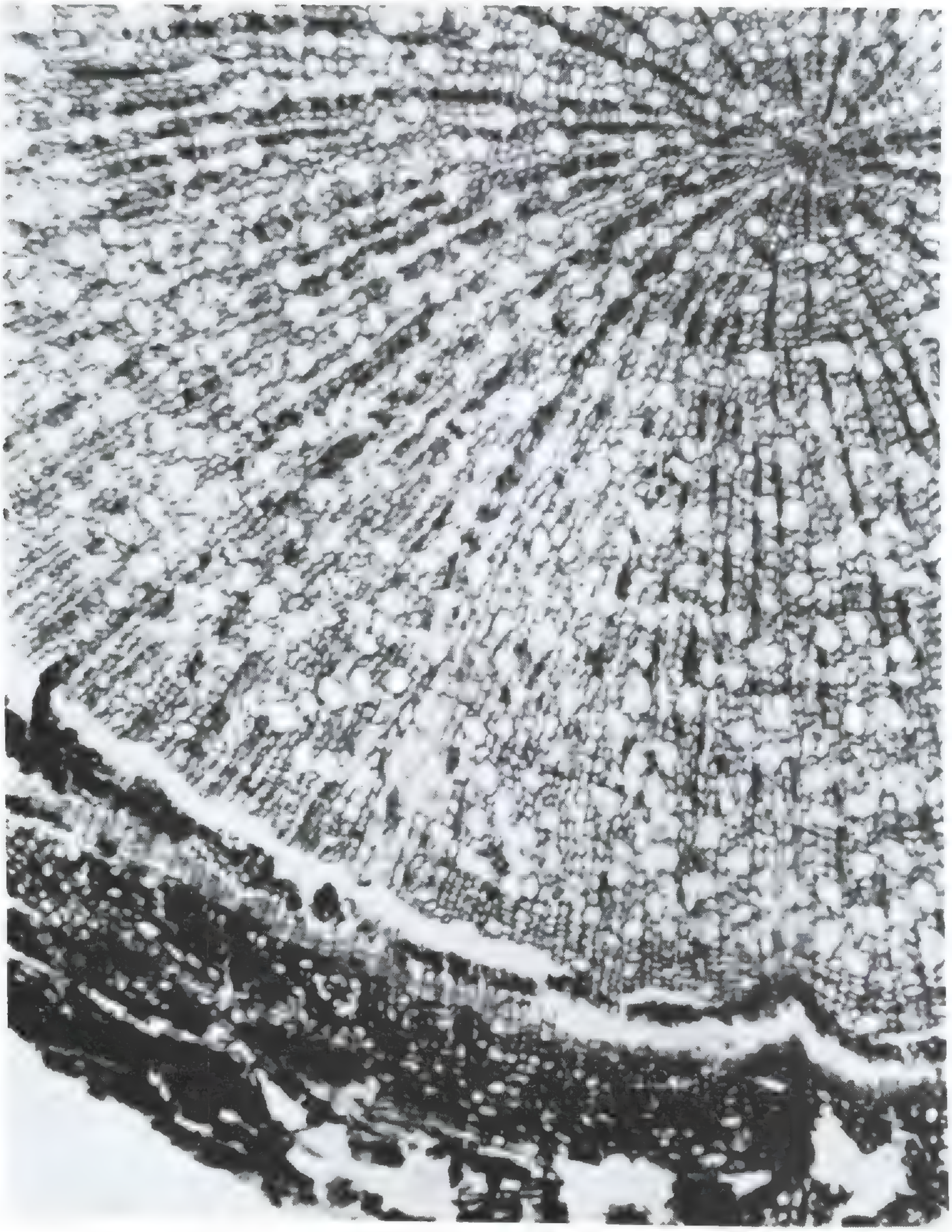

Figure 2. Cross-section of Root-shoot of *Vaccinium corymbosum* L. *(Vander Kloet 11271178).* Magnified 90 times.

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CAMP, W. H. 1945. The North American blueberries with notes on other groups of Vacciniaceae. Brittonia **5**: 203–275.

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BOOK REVIEW

KURATA, SATORU, AND TOSHIYAKI NAKAIKE, editors.
Illustrations of Pteridophytes of Japan. vol. 2. 648 pp. 1981. University of Tokyo Press. (Price 10,000 yen, approx. U.S. $50.00)

The strong phytogeographic relationship between the floras of the eastern United States and Japan is well-known. The relatively wide distributions of many genera and even species of pteridophytes is also familiar. These considerations make this sumptuously produced quarto-format volume of possible interest to the readers of Rhodora, *even though the text is entirely in Japanese.* Fortunately there are botanical names in Latin in the running heads and in the captions for the abundant illustrations and maps, also roman script signatures for some of the excellent drawings.

In this volume only a portion of the rich Japanese fern flora is covered, but for each species there are: a short descriptive text; a photo of the living plant; a full page drawing showing the whole plant and details of sori, venation, stipe cross-sections, scales, hairs, and even epidermal features, as appropriate for the species; a map showing the distribution in Japan; and a list of specimen citations, presumably those on which the dots on the maps are based. The book was done "with the cooperation of the Nippon Fernist Club".

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LITERATURE FOR NEW ENGLAND BOTANISTS

HEINRICH, BERND. 1979. *Bumblebee Economics*. viii + 245 pp. Harvard University Press, Cambridge, MA.

Lest the title mislead you, this book is not a treatise on beekeeping as business. Rather, the author reports on his extensive research experiments exploring biological energy costs and payoffs with bees as a model. He provides a fascinating and lucid account of how "bumblebees and their kin do what they do and what it means to each of them." Heinrich shows how bee physiology is related to energy balance, and how that in turn is related to pollination, and to the reproduction of plants. Of particular interest to New Englanders is the fact that many of his observations were made in Maine bogs and meadows, and interesting data for the interaction of bees with the native plants are presented. Heinrich hopes that the book will aid the reader in understanding "economic laws that are fundamental to success in living and that operate at all levels of biological organization from the molecular to the ecological."

CHAPMAN, RACHEL ROSS & GARRETT E. CROW. 1981. Raunkiaer's life form classification in relation to fire. Bartonia **48:** 19-33.

CHAPMAN, RACHEL ROSS & GARRETT E. CROW. 1981. Application of Raunkiaer's life form system to plant species survival after fire. Bull. Torrey Bot. Club **108** (4): 472–478.

Prescribed burning as a means of forest management control is presently receiving much attention. The authors evaluate the use of classifying the vegetation according to Raunkiaer's life forms system as a tool for predicting the effects of a prescribed burn on a given forest-type plant community. They found that Raunkiaer's classification will give a "first estimate of species survival after a prescribed fire." However other "modes of regeneration and recovery after fire" play an important role, and vary from species to species.

The longer *Bartonia* article gives more details of the experiments leading to their conclusions.

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Vol. 84, No. 838, including pages 159 315, was issued May 7, 1982.

Notice of Series Publication: Evolutionary Monographs

Attention is called to *Evolutionary Monographs*, a new series which is seeking papers. The scope of the papers, which are expected to be long ones, is evolutionary biology in the broad sense: ecology, floras, animal behavior, history and philosophy of the subject, and historical geology. "Probably most papers will be taxonomic, morphological, or geological." Anyone may submit the papers, and no payment is required. For further information write Evolution Monographs, University of Chicago, 915 E 57th St., Chicago, Il. 60637. The most recent volume published is:

SUNDELL, ERIC. The New World species of *Cynachum* L. Subgenus *Mellichampia* (A. Gray ex S. Wats.) Woods. (Asclepiadaceae). 1981. ii + 63 pp. Evolutionary Monograph **5,** University of Chicago, Chicago. Il. (Price $5.50)

RHODORA July 1982 Vol. 84, No. 839

CONTENTS

A monograph of the genus Malvastrum — III
Steven R. Hill 317

The composition, seasonal occurrence, and reproductive periodicity of the Phaeophyceae (brown algae) in New Hampshire
Arthur C. Mathieson and Edward J. Hehre 411

Studies on Mentha × dumetorum Schult. (Labiatae) to confirm its presumed parentage — M. aquatica Linn. × M. longifolia (Linn.) Huds.
B. O. B. Fagbemi and J. K. Morton 439

A note on the occurrence of root-shoots in Vaccinium corymbosum L.
S. P. Vander Kloet 447

Book Review: Illustrations of Pteridophytes of Japan 451

Literature for New England Botanists 452

Notice of Series Publication: Evolutionary Monographs . . . 453

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Cover illustration

Sagittaria cuneata, a northern species, is fairly common in northern New England, rarer to the South except down the Rockies. The species is variable, often producing flat, linear leaves similar to *Vallisneria americana* when growing submerged in rivers.

Original art by Pamela Bruns, reprinted here by permission from Hellquist, C. B., & Garrett E. Crow, *Aquatic Vascular Plants of New England. Part 3. Alismataceae*, New Hampshire Agr. Expt. Sta., UNH, Durham, N.H.

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REVISION OF TITHONIA

JOHN C. LA DUKE

ABSTRACT. *Tithonia* Desf. ex Gmelin is a genus distributed primarily in Mexico and Central America. The present treatment recognizes 13 taxa in 11 species, arranged in two sections. Chromosome counts are reported for 51 populations for 12 taxa of *Tithonia*. The genus is diploid at $n = 17$, with two taxa, *T. koelzii* McVaugh and *T. calva* var. *auriculata* La Duke, having B chromosomes. Numerical phenetics were used to help evaluate the morphological variation among the taxa. Fifty-eight characters were measured and evaluated using both cluster analysis and principal component analysis. These analyses resulted in a better understanding of subgeneric, specific, and subspecific groups. Phylogenetic reconstruction techniques were then used to develop hypotheses about the evolutionary relationships among the taxa. Using the phenetic and phylogenetic analyses, a subgeneric classification was proposed consisting of two sections, one of which has three series.

Collectors of Compositae in Mexico and Central America are usually familiar with the large, yellow or orange-rayed members of the genus *Tithonia*. Many species are weedy and sometimes dominate cultivated or fallow fields. Some taxa, such as *Tithonia diversifolia* (Hemsl.) A. Gray and *T. rotundifolia* (Mill.) S. F. Blake, are grown as ornamentals for their bushy stature and show of brilliantly colored flowers. The genus contains both annuals and perennials, and was last revised by Blake (1921) to include 10 species. Since that time, three taxa have been described, *T. pedunculata* Cronquist (Cronquist, 1965), *T. koelzii* McVaugh (McVaugh, 1972) and *T. hondurensis* LaDuke (LaDuke, 1982). Blake's (1921) revision was restricted to herbarium material and provided little insight into the evolutionary relationships among the taxa. The present study utilizes herbarium material, field observations, cytology, and numerical phenetics and cladistics, to provide data not only for a revision of the genus, but also for developing evolutionary hypotheses.

TAXONOMIC HISTORY

Tithonia was first described by Jussieu (1789). Jussieu referenced a presentation by Desfontaine which was to be published in Act. Paris extr. Vol. 12, but never appeared (Stafleu & Cowan, 1976; Desfontaine eventually did publish a generic description of *Tithonia* with the species *T. tagetiflora,* but not until 1802). Gmelin (1791) also cited this presentation of Desfontaine, and provided an additional generic description and a specific name, *T. uniflora.* The type species for the genus, *T. uniflora* Gmelin, however, must be called *Tithonia rotundifolia* (Miller) S. F. Blake, because *Tagetes rotundifolia* Miller (1768) is an earlier name for the same taxon.

Subsequently, a number of taxa in *Tithonia* were described and generic rearrangements made. In 1836, DeCandolle, in the Prodromus, recognized four species of *Tithonia.* Two of these, *T. pachycephala* DC. and *T. excelsa* (Willd.) DC., are now recognized as belonging to *Viguiera* (Blake, 1918). Schultz, in Seemann's Botany of the Voyage of the Herald (1856), described the subgenus *Mirasolia* to include the new taxon, *T. calva* Sch.-Bip. in Seemann. The subgenus *Mirasolia,* with two taxa, was proposed for generic status by Bentham and Hooker (1873), and all of *Tithonia* had four taxa. W. B. Hemsley (1881) recognized three taxa of *Mirasolia* and eight of *Tithonia.* Kuntze (1891) used the new generic name, *Urbanisol* (named after Dr. Ignaz Urban), and it included many of the taxa of *Tithonia.* This arrangement was proposed because he was a believer in absolute priority, and the name *Tithonia* had been used already by Linneaus in 1737 for *Rivina* L. (Phytolacaceae). He also retained *Mirasolia.* Blake (1918) moved a number of taxa of *Gymnolomia* into *Tithonia* and revised the genus in 1921, recognizing ten species and two subspecies.

In the present revision of *Tithonia,* I recognize many of the taxa of Blake (1921), the two new taxa described by McVaugh and Cronquist, and one recently described taxon. This gives eleven species (thirteen taxa) in two sections, as shown below:

Section *Tithonia*
Series Tithonia
Tithonia brachypappa B. L. Robinson
Tithonia rotundifolia (Miller) S. F. Blake
Tithonia thurberi A. Gray

Tithonia tubaeformis (Jacq.) Cass.
Series *Fruticosae* La Duke
Tithonia fruticosa W. M. Canby & J. N. Rose in J. N. Rose
Tithonia pendunculata A. Cronquist
Series *Grandiflorae* La Duke
Tithonia diversifolia (Hemsl.) A. Gray
Tithonia koelzii R. McVaugh
Section *Mirasolia* (Sch.-Bip. in Seemann) La Duke
Tithonia calva var. *calva* Sch.-Bip. in Seemann
Tithonia calva var. *auriculata* (Brandegee) La Duke
Tithonia calva var. *lancifolia* (B. L. Robinson & Greenm.) McVaugh
Tithonia hondurensis La Duke
Tithonia longiradiata (Bertol.) S. F. Blake

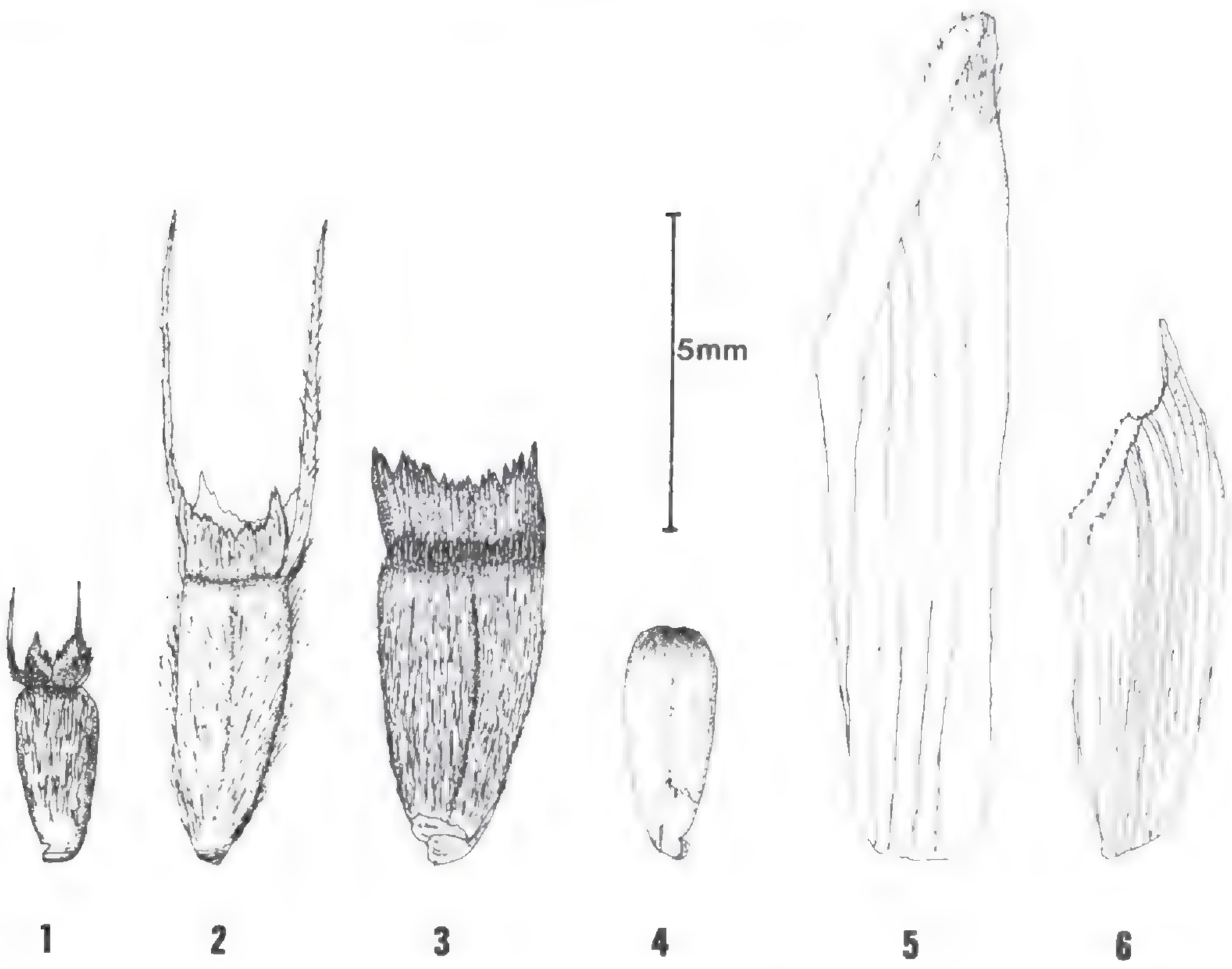
GENERIC AND SUBTRIBAL RELATIONSHIPS

Cassini (1829) placed *Tithonia* in the "Hélianthées section Rudbeckiées," with genera bearing superficial similarities (e.g. *Echinacea*). Lessing (1832) placed a number of the genera currently accepted as members of the Heliantheae in one of two tribes, "Senecionideae" or "Asteroideae." *Tithonia* was in the "Senecionideae subtribe Heliantheae [subdivision] Coreopsideae." The genera *Helianthus* L. and *Viguiera* H.B.K. were first allied to *Tithonia* at this time. DeCandolle (1836) followed Lessing (1832) at the tribal and subtribal level, but he added a number of taxa to his "Division Coreopsideae" which included *Tithonia*, *Viguiera*, and *Helianthus*. Bentham & Hooker (1873) recognized the tribe Helianthoideae, with ten subtribes, including Subtribe Verbesineae which, among other genera, contained *Gymnolomia*, *Helianthus*, *Mirasolia*, *Tithonia*, and *Viguiera*. Hoffmann (1890) followed this same basic concept. Stuessy (1977) recognized the legitimate subtribal name Helianthinae Dumort (Solbrig, 1963) for the group including *Helianthus*. This subtribe also retains *Gymnolomia* H.B.K., *Tithonia*, and *Vigueria* as members. The Verbesininae are suggested to include taxa close to *Verbesina* L.

The genera historically most closely related to *Tithonia* are *Gymnolomia*, *Helianthus*, and *Viguieria*. Some of the taxa in *Gymnolomia* were considered more than closely related to *Tithonia* by Blake

(1918), because he transferred many of them to *Tithonia*. Following these transfers, and others by Blake (1918), the genus *Gymnolomia* was reduced to four taxa, and no longer considered a close relative. Taxa of the genus *Helianthus* share similarities with some taxa of *Tithonia* such as habit, achene shape, and achene pubescence. *Helianthus*, however, produces a pappus of two awns which are readily deciduous, whereas *Tithonia* either does not produce a pappus or produces a nondeciduous pappus of a different nature. Other characters, such as the shape of the receptacle in fruit, which is convex in *Tithonia* and mostly flat in *Helianthus*, and the phyllary shape, linear to spathulate in *Tithonia* and usually obspathulate in *Helianthus*, further differentiate the two genera.

Blake (1918, p. 10) stated that the "origin of *Tithonia* as a Central American offshoot of some lost Viguieroid stock related to (subgenus) *Amphilepis* is more than probable." There are a number of large-headed taxa in subgenus *Amphilepis* and subgenus *Calanticaria* section *Hypargyrea*, which approach *Tithonia*. These taxa, which can be considered closely related to *Tithonia*, are *Viguiera excelsa* (Willd.) B. & H., *V. angustifolia* (H. & A.) S. F. Blake, *V. pachycephala* (DC.) Hemsl., *V. decurrens* A. Gray, *V. rosei* Greenm., and *V. hypargyrea* Greenm. The best character for differentiating these taxa from *Tithonia* is the nature of the peduncle. Penuncles of these *Viguiera* taxa may be thickened (e.g., *Viguiera excelsa, V. hypargyrea*), but they are cylindrical or angulate, and usually filled with pith. Another character differentiating these taxa is the nature of the pappus (Fig. 1–4.) Taxa such as *V. excelsa* and *V. pachycephala* are characterized by two awns and 4–10 scales (Fig. 1). These scales tend to be separate in these species, while in *Tithonia* the taxa are either without or with a pappus (Figs. 2–4). Of the latter, two types of pappus occur. First, a ring of basally and laterally fused squamellae occurs in *T. brachypappa* (sometimes reduced), *T. fruticosa*, and *T. koelzii* (Fig. 3). Second, awns are present, but again the squamellae are fused at least basally (Fig. 2). Taxa such as *V. decurrens, V. hypargyrea*, and *V. rosei* can be differentiated by the nature of the apex of the pales. The tip in these taxa is truncate and cupped, whereas those in *Tithonia* have acute to aristate-tipped pales (Figs. 5 & 6). Therefore, a number of characters are important in differentiating *Tithonia* taxa from its closest *Viguiera* relatives: 1) the flared (fistulose) hollow peduncle, 2) the nature of the pappus, and 3) the nature of the pales.



Figures **1–6**. Achenes (Figs. 1·4) and pales (5 & 6) of *Viguiera* and *Tithonia*. **1.** *V. excelsa (Cronquist 9791,* TEX); **2,** *T. tubaeformis (La Duke et al. 406,* OS); **3,** *T. fruticosa (Weber & Bye 8352,* voucher grown from seed, OS); **4,** *T. calva* var. *calva (Cronquist 10550,* MICH); **5,** *V. rosei (McVaugh 896,* OS); **6,** *calva* var. *calva (Cronquist 10550,* MICH). All same scale.

CYTOLOGY

Chromosome numbers from the taxa of *Tithonia* were determined for either mitotic or meiotic material using standard techniques of killing, fixing, and staining (Snow, 1963; Stuessy, 1971; Jackson, 1973).

Twelve of the thirteen taxa of *Tithonia* have been examined from 51 populations. Five taxa are reported here for the first time. Most populations are $n = 17$ ($2n = 34$), but variation does occur (Table 1), primarily in the presence of B-chromosomes. *Tithonia calva* var. *auriculata* preparations had $2n = 34 + 4$B's, while the B-complement in *T. koelzii* varied from 4 to 5 per cell in addition to the normal complement. In previous studies of B-chromosomes, correlations were made between the number of B's with adaptation to climate (Frost, 1958), stress (Rees & Hutchinson, 1973), and chiasmata fre-

Table 1. Chromosome numbers in *Tithonia*.

Taxon	Chromosome Number		Number of Populations Sampled, and/or Reference
	n	2n	
T. brachypappa	17[a]		3[b]
T. calva var. *calva*	17		3; Solbrig et al. 1972, (as *T. auriculata;* Keil & Pinkava, 1976.
		34	1; Turner & Flyr, 1966.
T. calva var. *auriculata*		34+4B[a]	1
T. diversifolia	17		5; Powell & King, 1969; Solbrig et al., 1972.
	15		Mehra & Remanandan, 1969.
		34	Turner, Ellison & King, 1961.
T. fruticosa		34[a]	1
T. hondurensis	17[a]		1
		34[a]	1
T. koelzii	17+6B[a]		1
		34+5B[a]	1
T. longiradiata	17		3
		34	Turner, Powell, & King, 1962; Turner, Ellison, & King, 1961
T. pedunculata	17		1; Solbrig et al., 1972.
		34	1
T. rotundifolia	17		5; Subramanyam & Kamble, 1967; Sarkar et al., 1978; Gupta & Gill, 1979.
		34	5; Turner & King, 1964; Bilquez in Delay, 1951; Heiser, 1948.
		32	Vilmorin & Chopinet, 1954.
T. thurberi	17		Keil & Powell, 1976.
		34	1
T. tubaeformis	17		12; Solbrig et al., 1972; Keil & Stuessy, 1977.
	ca.17		1
		34	6; Turner & Johnston, 1961; Turner, Ellison, & King, 1961; Heiser & Smith, 1955.

[a] *First report*

[b] *Populations sampled are labeled with an asterisk (*) in the representative specimen section following each taxon.*

quency (Cameron & Rees, 1967; Vosa & Barlow, 1972). Due to the limited material of both of these taxa, correlations of this sort have not been possible. Therefore, the role that B-chromosomes have played in the speciation and evolution of the taxa is difficult to assess.

The taxa in *Viguiera* most closely related to *Tithonia* are unknown cytologically. The base number, however, for the genus is $n = 8$ or 17 (Jansen & Stuessy, 1980), with most of the taxa being $n = 17$. Similarly, *Helianthus* is based on $n = 17$. These data are not useful, therefore in differentiating *Tithonia* from these genera, but they do indicate a close tie among all three.

ISOLATING MECHANISMS

The absence of polyploidy in *Tithonia* suggests that speciation has occurred only at the diploid level. Isolating mechanisms that are operating to preserve the species in *Tithonia* are primarily of two types: 1) spatial isolation and 2) reproductive isolation (Levin, 1978). Spatial isolation is probably the primary mode, with most of the taxa occurring in areas geographically isolated from each other. In most cases of geographical overlap, the taxa are isolated by habitat differences. Two pairs of taxa have been collected sympatrically: *T. diversifolia* with *T. longiradiata*, and *T. tubaeformis* with *T. rotundifolia*. The population of *T. diversifolia* and *T. longiradiata (La Duke et al. 535 & 536)* in Guatemala had no detectable intermediates. The exact mode of reproductive isolation is not clear. However, since no F_1 hybrids were detected and these taxa flower at the same time, the isolating mechanism has been narrowed to one of the following modes (from Levin, 1978): 1) Floral divergence, 2) reproductive mode, 3) cross-incompatibility, or 4) hybrid inviability or weakness. None of these can be eliminated at this time, as any of them are equally probable.

Isolation in the second pair of sympatric species, *Tithonia tubaeformis* and *T. rotundifolia* is somewhat easier to explain. Samples from two mixed populations (*La Duke et al. 510, & 511; Stuessy & Gardner 4093, & 4094*) indicate that hybridization to the F_1 level has occurred. Pollen stainability using lactophenol cotton blue (Hauser & Morrison, 1964) showed a putative hybrid from *La Duke et al. 510* and *511* with 23% stainable pollen (200 grains sampled). Parental pollen was 98.5% for *T. rotundifolia* and 99% for *T. tubaeformis*.

The isolating mechanism in this case, therefore, is hybrid sterility, a mode frequently encountered in interspecific crosses (Levin, 1978).

CONCEPTS OF SPECIES, VARIETIES, AND SECTIONS

The species concept used in this study is a phenetic one (Sokal and Crovello, 1970). No data are available, other than those mentioned above, concerning the crossability of the taxa, so a biological species concept (Mayr, 1963) cannot be utilized totally. However, the genetic isolation cited above does support a biological species concept. The numerical taxonomic study, to be discussed later, demonstrates two important ideas: (1) the taxa of *Tithonia*, as represented by populational samples, are cohesive groups; and (2) these cohesive taxa are well differentiated from each other using morpological criteria.

Both subspecies and variety are frequently used as subspecific categories in botanical systematic studies. Historically, however, there has been less distinction between taxa at the varietal rank than between taxa at the subspecific rank (Kapadia, 1963; Burtt, 1970). The amount of differentiation between the three subspecific taxa in *T. calva* is relatively small, but geographically consistent; therefore, the rank of variety has been chosen to indicate this minor difference.

Sections are used instead of subgenera in this treatment because the differences between the two main groups of taxa in *Tithonia* are believed to be less than those reflected ordinarily by the rank of subgenus.

NUMERICAL TAXONOMY

Historically, *Tithonia* is a relatively small group of taxa (10 species recognized by Blake, 1921). However, there is confusing morphological diversity in some parts of the genus at both the populational and specific levels. First, two taxa, *T. diversifolia* and *T. rotundifolia*, are quite similar in a number of features and these have been misidentified in a number of recent publications (Pal et al., 1976; Herz & Sharma, 1975). Second, one of Blake's (1921) species, *T. auriculata*, is difficult to distinguish from *T. calva* var. *lancifolia*, differing primarily in morphology of the leaves. Third, a number of populations of *T. longiradiata* in Honduras and Belize are different in having smaller heads, and strongly revolute leaf margins, and may represent a different species. Fourth, there have been no clearly

defined subgeneric groups to help provide a better understanding of the most closely related taxa.

To assist in resolving the taxonomic problems mentioned above, methods of computer-assisted numerical taxonomy were used. Earlier workers have suggested that the use of numerical techniques should be part of routine taxonomic studies (e.g., Gilmartin & Harvey, 1976). The concept of numerical taxonomy has progressed from simple comparisons of similarities and differences to more sophisticated multivariate techniques (for a review, see Sneath & Sokal, 1973). Numerical techniques can be useful in understanding the distribution and amount of variation of morphological characteristics (McNeill, 1979). Methods such as clustering or principal component analysis (PCA) can assist in developing taxonomic concepts, but they do not themselves define the subgeneric, specific, or subspecific boundaries. Each analysis must be carefully interpreted, and can only serve as a guideline in taxonomic delimitations.

The purpose of this section is to summarize the similarities and differences among the taxa to determine particularly: 1) the morphological integrity of *Tithonia diversifolia*, *T. longiradiata*, and *T. rotundifolia*, 2) the relationships of *T. auriculata* to *T. calva* var. *lancifolia*, and 3) differentiation of all taxa from each other and their placement in subgeneric groups.

MATERIALS AND METHODS

Fifty-nine populations were measured from herbarium material for 58 characters (Table 2; data available from author). The number of populations sampled per taxon was based on 1) the amount of material available for each taxon, and 2) the amount of obvious variation present in each taxon. Quantitative characters were scored for each OTU (operational taxonomic unit, Sokal & Sneath, 1963; here a population) as the highest measure for that trait for each population sample. This was believed to be a better approach than using a mean or low number because it indicates the maximum genetic potential of each character. Following the populational computations, relationships among the individual taxa were determined using the average values for each taxon for the quantitative characters and the most common value for qualitative characters.

The techniques used in the analysis of these data were those contained in the NT-SYS package (Rohlf et al., 1972). Data were

Table 2. Characters and character states of *Tithonia* used in the numerical study. Numbers in parentheses indicate values for qualitative states or scale for quantitative measurements.

Habit and Stem. 1. Habit; herb (0), shrub (1), tree (2). **2.** Height (m). **3.** Stem pubescense: glabrous to sparse (0), moderate (1), dense (2).

Leaves. 4. Petiole length: sessile to 10 mm (0), 11–20 mm (1), 21 or greater (2). **5.** Leaf outline: linear (0), lanceloate (1), triangular (2), ovate (3), deltate (4), triangular or lanceolate and 3 5 lobed (5). **6.** Leaf base: cuneate (0), attenuate (1), attenuate-auriculate (2). **7.** Leaf color: above and below the same (0), above and below different (1). **8.** Leaf length (mm). **9.** Leaf width (mm). **10.** Leaf pubescence above: glabrous to sparse (0), moderate (1), woolly (2). **11.** Leaf pubescence below: glabrous to sparse (0), moderate (1), woolly (2).

Heads. 12. Nature of the peduncle: bract present (0), bract absent (1). **13.** Peduncle length (mm). **14.** Peduncle pubescence: glabrous to sparse (0), moderate (1), dense (2). **15.** Peduncle diameter (mm). **16.** Peduncle shape: constricted (0), even (1).

Phyllaries. 17. Total number of phyllaries. **18.** Number of phyllary series. **19.** Outer phyllary series length (mm). **20.** Outer phyllary series width (mm). **21.** Inner phyllary series length (mm). **22.** Inner phyllary series width (mm). **23.** Outer phyllary tip: round (0), pointed (1). **24.** Inner phyllary tip: round (0), pointed (1).

Ray florets. 25. Number of ray florets. **26.** Ray floret color: yellow (0), orange (1). **27.** Ray corolla length (mm). **28.** Ray corolla width (mm). **29.** Ray tube length (mm). **30.** Ray tube width (mm). **31.** Pappus present (0), absent (1).

Pales. 32. Pale length (mm). **33.** Pale tip length (mm). **34.** Pale width (mm). **35.** Pale texture: indurate (0), smooth (1). **36.** Vesture of pales: glabrous (0), pubescent on fold (1), pubescent on apical surface and fold (2), pubescent on edge (3). **37.** Pales enclosing achenes: loosely (0), tightly (1).

Disk florets. 38. Disk floret number. **39.** Disk throat length (above swollen base) (mm). **40.** Disk throat width (above swollen base) (mm). **41.** Disk tube length (mm). **42.** Disk tube width (mm). **43.** Base of throat length (mm). **44.** Base of throat width (mm). **45.** Disk lobe length (mm). **46.** Disk floret pubescence: base of throat (0), tube (1), base of throat and tube (2). **47.** Anther length (mm). **48.**

Anther color: black (0), brown or tan (1). **49.** Style branch length (mm). **50.** Style length (mm). **51.** Base of style: ovarian disk (0), swollen base (1), ovarian disk and swollen base (2).

Achenes (disk). **52.** Achene shape: rounded quadrangular (0), quadrangular (1), triangular (2). **53.** Achene color: black (0), brown (1), black or brown (2). **54.** Achene pubescence: absent (0), present (1). **55.** Achene length (mm). **56.** Achene width (mm). **57.** Pappus: none (0), squamellae (1), awns and squamellae (2).

Receptacle. 58. Diameter (mm).

standardized using the STAND subroutine resulting in a mean of zero and a standard deviation near unity. Correlation and distance matrices were computed using SIMINTVL. Cluster analyses were performed using the TAXON subroutine. Three techniques, single linkage, complete linkage, and unweighted pair group method using arithmetic averages (UPGMA), were used to evaluate both correlation and distance matrices. A cophenetic correlation coefficient was calculated following each clustering routine to determine the amount of distortion the phenogram showed relative to the relationships in the matrices. In addition to clustering, principal component analysis (PCA) was used to evaluate the data (Harmon, 1967). The subroutine FACTOR was used and both unrotated and rotated (Kaiser, 1958) (using VARIMAX) components were output. A minimum spanning tree was used with the PCA to detect distortion (Rohlf, 1970).

RESULTS AND DISCUSSION

Analysis of Populations. The similarities and differences of the genus have been summarized using two techniques: 1) cluster analysis, and 2) PCA. The cluster analysis technique which best summarizes the relationships between populations based on the highest cophenetic correlation coefficient (.86) is UPGMA (Fig. 7). The pairwise relationships of particular taxa were well illustrated. Populations of *Tithonia diversifolia* and *T. rotundifolia* formed clusters among themselves and were not grouped near each other (Fig. 7). They were, in fact, placed in different subgroups. The four populations (UK 1–4) from Honduras and Belize were also well resolved. These populations were grouped closely together but they tie in

most closely to the populations of *T. longiradiata* (Fig. 7). Lastly, the similarity value between *T. auriculata* and *T. calva* var. *lancifolia* was quite high (Fig. 7). Two populations of *T. auriculata* clustered more closely with populations of *T. calva* var. *lancifolia* than with the third population of *T. auriculata.*

The cluster analysis also depicted the populational groups as well differentiated from one another (Fig. 7). Each taxon formed by a cluster of populations was grouped with another populational cluster at a much lower level. Most species pairs were grouped at the .35 level or lower. The pair representing *Tithonia longiradiata* and the unknowns (1 4) clustered at a slightly higher level (.39). These taxa represent morphologically more similar groups. At a somewhat lower level of clustering (−.19), the genus is divided into two subgroups of taxa. One group includes *T. calva* var. *calva, T. calva* var. *lancifolia, T. auriculata, T. longiradiata,* and the Honduras and Belize populations. The remaining taxa make up the second subgroup.

The PCA of these same populations resulted in the relationships depicted in Figure 8. In the first two principal components, which account for 37% of the variation, most of the population groups representing the same taxon are well differentiated (Fig. 8). The problem taxa, *Tithonia diversifolia* vs. *T. rotundifolia,* and *T. longiradiata* vs. UK 1 4, were as easily distinguished as they were in the cluster analysis. In addition, the *T. auriculata* populations and the *T. calva* var. *lancifolia* populations are close to each other. Adding the third component (9.7% of the variation) primarily separates the taxon *T. tubaeformis* from the others (Fig. 9). The rotated PCA resulted in essentially the same relationships in space and therefore are not presented. The PCA also clearly differentiated the two subgroups of taxa formed by the cluster analysis.

Analysis of Taxa. The analysis of the taxa gave somewhat different results concerning their pairwise similarities. The UPGMA technique again gave the highest cophenetic correlation coefficient (.87), but those taxa which were clustered most closely in the populational study were not those clustered together in this analysis (Fig. 10). Specifically, two taxa, *Tithonia fruticosa* and *T. pedunculata,* are those which differ in their relationships with other taxa. *Tithonia pedunculata* is most closely clustered with *T. tubaeformis,* and *T. fruticosa* with the group including *T. calva* (+ 2 vars.), *T. auricu-*

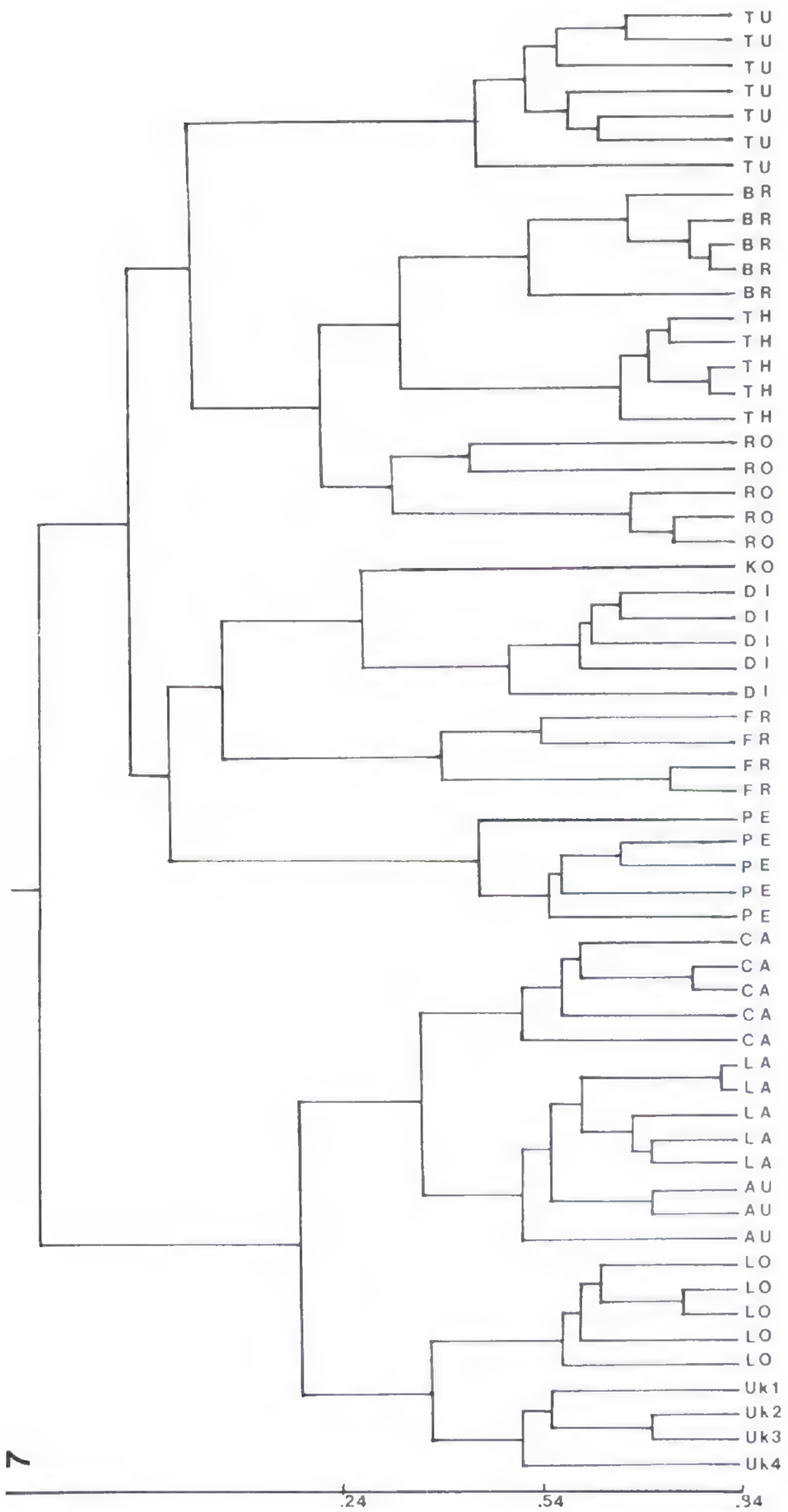
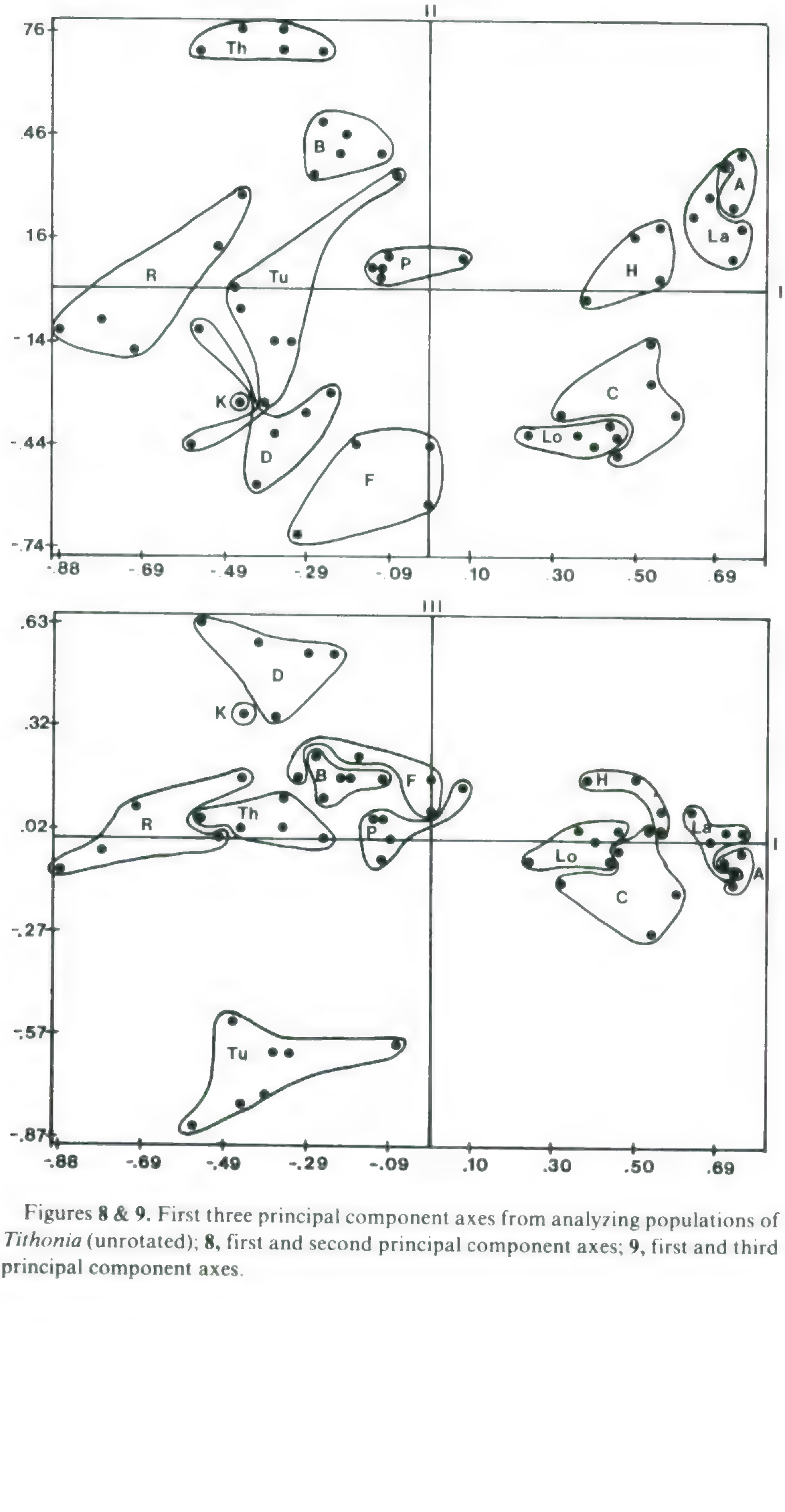


Figure 7. Phenogram of population of *Tithonia* using UPGMA. Taxa are abbreviated using the first two letters of the specific or varietal epithet (see Table 4). Uk 1–4 are populations from Belize and Honduras of uncertain affinity. Scale is the level of correlation.



Figures **8 & 9.** First three principal component axes from analyzing populations of *Tithonia* (unrotated); **8,** first and second principal component axes; **9,** first and third principal component axes.

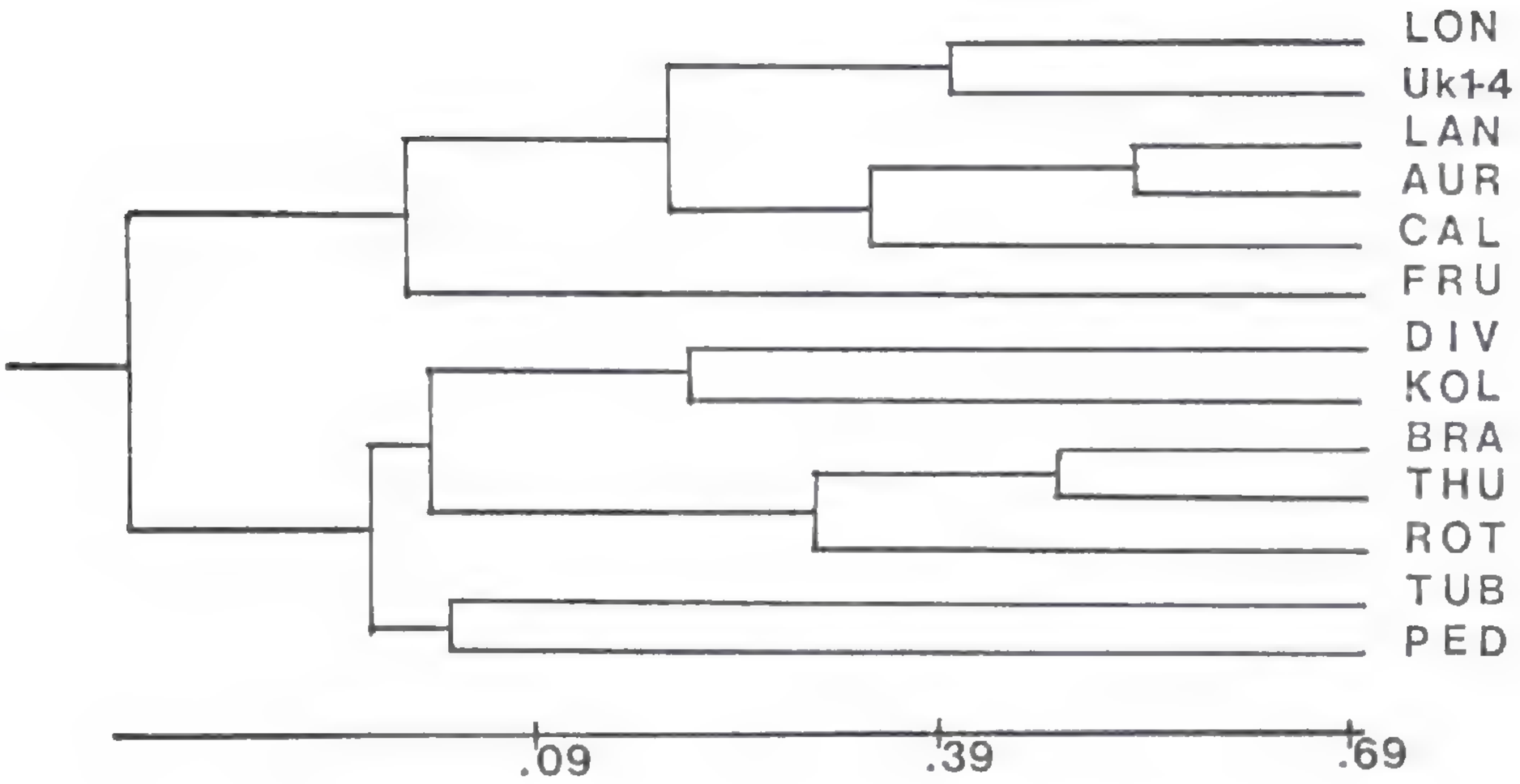


Figure **10.** Cluster analysis (UPGMA) of summarized data for taxa of *Tithonia*. Scale is level of correlation.

lata, UK 1–4, and *T. longiradiata.* The level of clustering was very low in both cases (less than .09) indicating that these are not strongly similar taxa, but are instead placed here based on very few similarities. These distortions may occur due to the summarization of the data by averaging the values for quantitative characters and taking the most common state for qualitative characters. This summarization of data for each taxon reduces the variation present in each taxon, and the similarities and differences are distorted.

The PCA results were quite similar to those obtained in the cluster analysis (Fig. 11). Three-dimensional PCA is sometimes difficult to interpret, because it is known to distort close relationships (Rohlf, 1970). The MST helps reveal these areas of distortion. For instance, *Tithonia calva* (+ 2 vars.), *T. auriculata, T. longiradiata,* and UK 1–4 on the plot of the first three principal components appear close to each other and the MST supports these relationships. The relationship of *T. fruticosa* with *T. koelzii,* as shown by the MST, is similar to that in cluster analysis (Fig. 7). Again, the relationships of *T. pedunculata* with an annual taxon, in this case *T. thurberi,* is not consistent with any of the previous analyses. An additonal relationship which is evident from this analysis, as well as the cluster analysis and PCA of populations, is that two main groups of taxa are formed: one group including *T. calva* (+ 2 vars.), *T. longiradiata, T. auriculata,* and the Honduras and Belize populations; and the second group the remaining taxa.

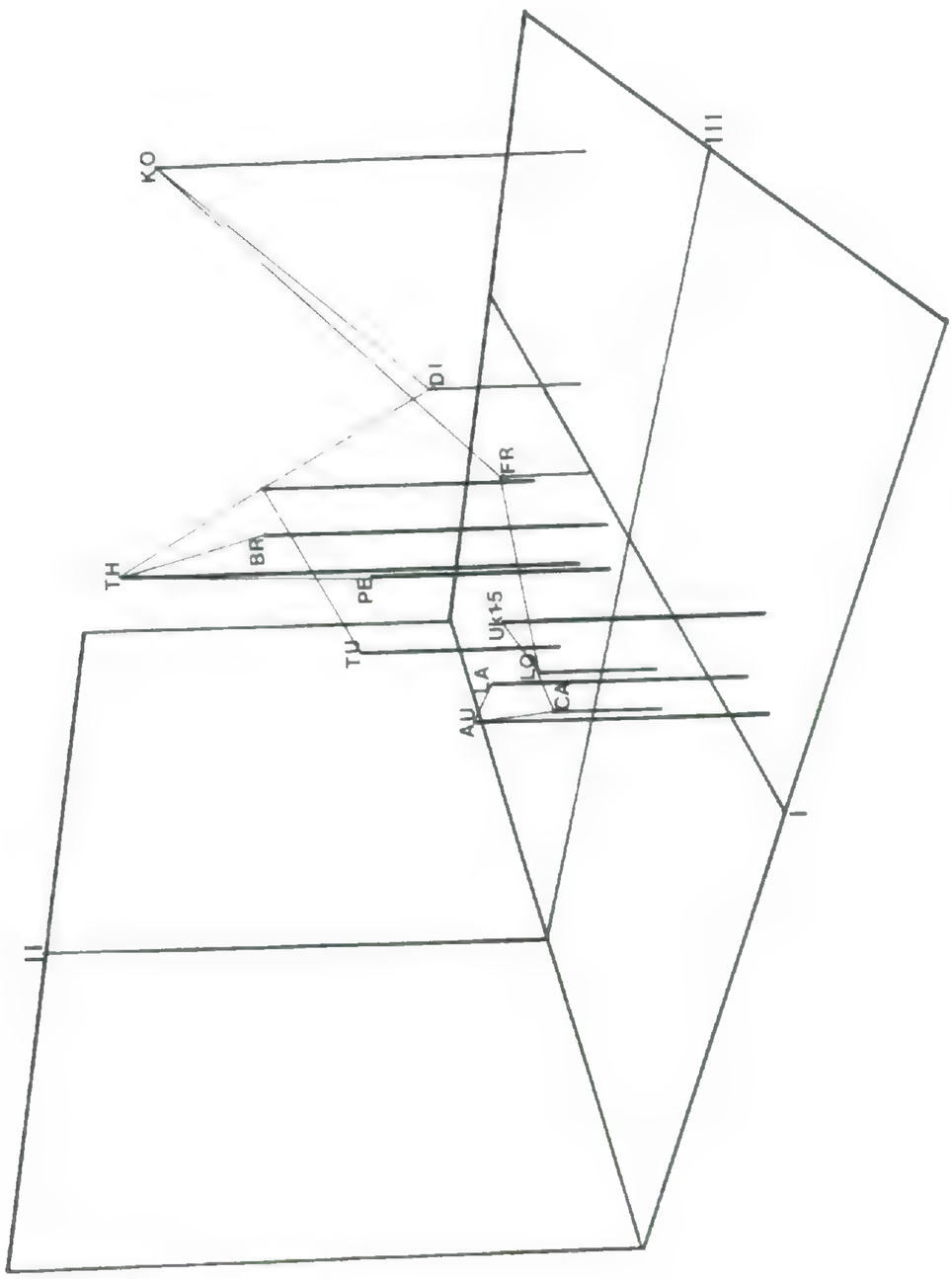


Figure 11. Principal component analysis (unrotated) in three dimensions of data for taxa of *Tithonia*. Minimum spanning tree is overlain.

CONCLUSIONS

A number of patterns of variation can be resolved from these anlayses. First, the populations of *T. longiradiata* from Honduras and Belize should be recognized at the rank of species. This taxon has already been described elsewhere as *T. hondurensis* La Duke (La Duke, 1982) to prevent a *nomen nudum* from occurring in a paper published prior to this revision. These populations are grouped together consistently and possess a set of characters which differentiate them at a level warranting the rank of species. Second, the two taxa, *T. diversifolia* and *T. rotundifolia,* can be consistently differentiated from one another and should be retained at the rank of species. Third, the taxon *T. auriculata* should be given the rank of variety under *T. calva* (called *T. calva* var. *auriculata;* see taxonomic section). The characters which differentiate it from its closest relative, *T. calva* var. *lancifolia* are minor and the level of clustering supports this similarity. Fourth, two subgroups can be delimited within the genus as follows: 1) *T. calva* (and its 3 vars.), *T. hondurensis,* and *T. longiradiata;* and 2) the remaining eight taxa. These patterns of variation suggest that two subgeneric taxa should be recognized.

PHYLOGENETIC RECONSTRUCTION

The development of phylogenetic hypotheses has been part of botanical revisionary studies for many years (e.g. Canne, 1977; Stuessy, 1978). However, the documentation of methods and interpretation of the resultant phylogenetic diagrams have not always been adequate (Funk & Stuessy, 1978). Three steps are important in phylogenetic reconstruction: 1) the choice of units to use in the evolutionary analysis, 2) the selection of characters and states, and their polarity, and 3) the choice of a method to evaluate these data. Superficially, these steps seem straightforward, but controversy exists concerning the theory behind each.

The choice of evolutionary units is the first step in phylogenetic reconstruction, and it depends on the questions being asked. In the case of *Tithonia,* the interest is in the evolutionary relationships among the taxa. Consequently, the taxa become the evolutionary units.

The choice of characters, states, and the determination of polarity is more difficult. Characters and character states are usually easily

determined for qualitative characters and somewhat more difficultly for quantitative characters since discrete character states are not usually evident. The characters are not useful, however, unless the evolutionary polarity for each can be hypothesized. The different methods of determining character polarity have been recently reviewed (Crisci and Stuessy, 1980; Watrous & Wheeler, 1981). Many of the methods which have been proposed are not applicable to *Tithonia* (i.e., fossils), or have a low confidence level (i.e., ingroup common equals primitive). One effective method for polarity determination is the related-group (or outgroup) criterion (Kluge & Farris, 1969; Lundberg, 1972). Related-group comparison has the following assumptions. First, the most closely related taxon or group of taxa to the one in question can be estimated. In the case of *Tithonia*, the outgroup consists of members of *Viguiera* subgenus *Amphilepis* and subgenus *Calanticaria*. Second, a character state which is shared by the outgroup and the taxon being investigated is regarded as ancestral. Since the two groups shared a common ancestor most recently, it is logical that any changes from the primitive form will show in one of the two ancestors. This technique was used in character polarity determination.

The last step, choice of method, is also somewhat controversial. The basis for many of the methods of phylogeny reconstruction, stem from Hennig (1950, 1966). Hennig detailed a theoretical basis for phylogenetic reconstruction, and applied these to specific organisms. Expansion of these ideas and possibly more importantly, the advancement of new ideas of phylogeny reconstruction has led to numerous techniques for evaluation of evolutionary data. These techniques include: Prim networks (Prim, 1957), the Weighted Invariant Step Strategy, WISS (Farris et al., 1970), the clique, or character compatibility method (LeQuense, 1969, 1972; Estabrook et al., 1975, 1976a, b), and Wagner methods (Kluge & Farris, 1969; Farris, 1970). Considerable literature exists concerning the validity of each of these techniques (for review see Funk & Stuessy, 1978; Farris & Kluge, 1979), and two main schools predominate: 1) character compatibility, and 2) parsimony. Character compatibility removes those characters which show reversals or parallelisms, and may result in incomplete resolution of small groups of taxa. The technique does not make estimates of the best fit for parallelisms or reversals in character trends, but instead leaves those judgments for

the biologist studying the group. The parsimony technique minimizes the parallelisms and reversals to produce a more resolved diagram of the relationships. For this reason, a representative technique from each group has been utilized in this study; the character compatibility technique of Estabrook et al. (1975, 1976a, b); and the parsimony technique of Farris (1970) (Wagner 78 version).

The purpose of these analyses is to: 1) develop hypotheses as to character trends in *Tithonia*, 2) utilize character compatibility and parsimony to evaluate the phylogenetic relationships, and 3) compare these results with the relationships determined by the numerical taxonomic techniques to help produce an even more predictive classification.

MATERIALS AND METHODS

The characters which were initially evaluated were those used in the numerical taxonomic study. Most of the quantitative characters were not used because accurate discontinuities could not be detected in the data which could be evaluated evolutionarily. No character states which were unique to only one taxon were used because they do not give information about the between-taxa relationships; they only reinforce the unique nature of the species. The outgroup used for determining the polarity of the character trends were taxa from the subgenera *Amphilepis* and *Calanticaria* of *Viguiera*. These taxa were chosen because, within *Viguiera*, they form the most closely related group to *Tithonia*. Fourteen characters finally were selected for use in the analyses (Table 3).

The determination of two of these characters is somewhat difficult and a brief explanation is in order. There are two types of leaf attachments, sessile and petiolate, in *Tithonia*, sessile being advanced. The leaf bases on these leaves are either auriculate or not, but the auriculae are not of the same nature on sessile and petiolate leaves. In the former, they are persistent, and in the latter, they are ephemeral (in the sense that the auriculae may not always be produced on each leaf, and if produced, may rapidly dry and brown). The nature of the pappus is the second difficult character set. Achenes in *Tithonia* are of three types (Fig. 2–4): epappose, a pappus of fused squamellae, or a pappus of squamellae plus two awns. The outgroup has squamellae plus awns (Fig. 1). I view these characters in the following way: one character is the presence or absence

Table 3. Characters and character states used in the phylogenetic reconstruction of *Tithonia*.

Character	Character State	
	Ancestral (A)	Derived (D)
1. Duration	perennial	annual
2. Leaf attachment	sessile	petiolate
3. Persistent auriculae of leaf base	absent	present
4. Ephemeral auriculae of leaf base	absent	present
5. Leaf shape	linear to deltate	3-5 lobed
6. Nature of the peduncle	unconstricted	constricted
7. Ray ligule length	short	long
8. Number of series of phyllaries	2-3	4
9. Pale length	short	long
10. Anther color	black	brown
11. Achene shape	triangular or quadrangular	rounded quadrangular
12. Achene vesture	pubescent	glabrous
13. Pappus	present	absent
14. Nature of Pappus	with awns or absent	only fused squamellae

of pappus, with the absence being derived, and the other character is the specialized nature of the pappus in the taxa with fused squamellae, but lacking awns. I view this as a derived character state independent of the loss of pappus. It may be argued that the four characters of leaves and pappus might better be regarded as transformational series of only two characters. An hypothesis for the leaf transformation would begin with the petiolate condition as primitive, the petiolate plus auriculate condition as derived in one direction and the sessile condition in the other. The sessile, auriculate condition is then further derived from the sessile condition. Similarly, one might hypothesize that the pappus transformation has gone from achenes with squamellae plus awns as primitive, and the epappose and squamellar conditions as derived in opposite direc-

tions from it. To evaluate these possibilities, these trends were also employed in the analysis. The data matrix of the fourteen characters is presented in Table 4 (showing the first leaf and pappus trends only). Both character compatibility and Wagner 78 were used to evaluate these data.

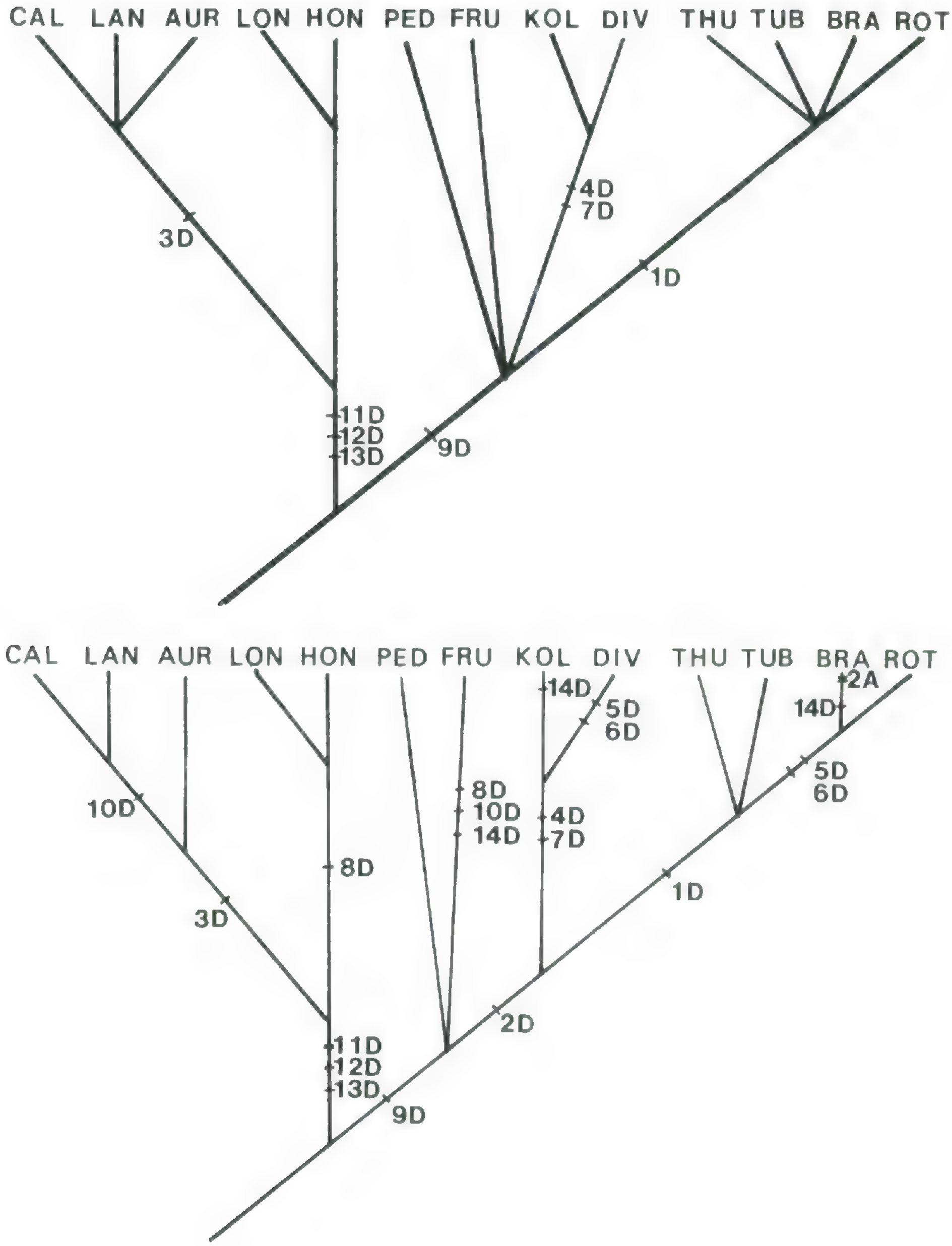
Table 4. Data matrix for the phylogenetic reconstruction of *Tithonia*. 0 = ancestral, 1 = derived.

Taxon	Characters													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
T. brachypappa	1	1	0	0	1	1	0	0	1	0	0	0	0	1
T. calva var. *auriculata*	0	1	1	0	0	0	0	0	0	0	1	1	1	0
T. calva var. *calva*	0	1	1	0	0	0	0	0	0	1	1	1	1	0
T. calva var. *lancifolia*	0	1	1	0	0	0	0	0	0	1	1	1	1	0
T. diversifolia	0	0	0	1	1	1	1	1	1	0	0	0	0	0
T. fruticosa	0	1	0	0	0	0	0	1	1	1	0	0	0	1
T. hondurensis	0	1	0	0	0	0	0	1	0	0	1	1	1	0
T. koelzii	0	0	0	1	0	0	1	0	1	0	0	0	0	1
T. longiradiata	0	1	0	0	0	0	0	1	0	0	1	1	1	0
T. pedunculata	0	1	0	0	0	0	0	0	1	0	0	0	0	0
T. rotundifolia	1	0	0	0	1	1	0	0	1	0	0	0	0	0
T. thurberi	1	0	0	0	0	0	0	0	1	0	0	0	0	0
T. tubaeformis	1	0	0	0	0	0	0	0	1	0	0	0	0	0

RESULTS AND DISCUSSION

The character compatibility technique produced two trees, both using eight of the 14 characters. Both diagrams used the following seven characters: 3, 4, 7, 9, 11, 12, and 13. Character 1 was used in organizing one tree (Fig. 12) while character 2 was used in the other. Since both of the trees used the same number of characters with only one difference between them, each tree is judged equally acceptable. One of these trees (Fig. 12) was, however, chosen for comparison with the diagram produced by the parsimony technique (Fig. 13) because of their similarity.

The parsimony technique has a higher level of resolution (Fig. 13). In this technique, all the characters are utilized in constructing the phylogenetic diagram. Five characters exhibit parallel evolution in this group based on the most parsimonious arrangement of the



Figures **12 & 13.** Cladograms of taxa of *Tithonia* based on character compatibility (**12**) and Wagner 78 (**13**) analyses. Changes in characters on the tree from the ancestral to the derived (D) state are indicated by number (See Tables 3 and 4). Refer to Table 4 for complete names of taxa. One reversal occurs in character 2(A) in Fig. 13 (double bar).

characters. The derived character states for these characters are: 3–5 lobed leaved (5D), constricted peduncle (6D), 4 phyllary series (8D), brown anthers (10D), and pappus of fused squamellae (14D). The parallel nature of each of these states can be traced in Fig. 13. Only one character shows a reversal and that is the nature of the leaf attachment (2). Petiolate leaves is the derived state of this character and serves to unite seven of the basal taxa, but the taxa forming the group *Tithonia diversifolia, T. koelzii, T. rotundifolia,* and *T. tubaeformis* all have petiolate leaves. Since the primitive condition is sessile the trend reverses with *T. brachypappa.*

Utilizing the alternate character trends for the nature of the pappus and leaf attachment, the results are more complex than those already presented for both techniques. The character compatibility program used only five of the now twelve characters resulting in larger unresolved clusters of taxa. The parsimony technique produced a diagram with a greater number of necessary character changes and increased the amount of parallelism and reversal in the tree.

A number of evolutionary groups are evident from these analyses. First, two main groups diverged early. One group includes the three taxa, *Tithonia calva* (+ 3 vars.), *T. hondurensis,* and *T. longiradiata.* This group shares a number of important achene character states (11, 12, 13). The other group of the remaining taxa is united based on the nature of the pales. This group can be further subdivided into three evolutionary lines. One line includes the two taxa *T. fruticosa* and *T. pedunculata.* These are united with this large group based on the nature of the pales, but do not share derived states of other characters with individual members of the group. Therefore, the position of these two taxa early in the evolution of the line is required. Using numerical techniques, these two taxa are quite similar, but they are problem taxa even with these methods. Given new data, the resolution of this multiple branch on the diagram may be possible.

Tithonia diversifolia and *T. koelzii* form a second group. These taxa are united based on two unique character states. One is the nature of the auriculae. Logically, the evolution of this unusual character state on two separate lines is not as probable as its occurrence in the ancestor of two closely related taxa. These two taxa also share the trait of longest ray florets in the genus.

The last group has the advanced trait of all being annuals. These four taxa are quite similar morphologically and the monophyletic origin of the annual habit would support these similarities. *Tithonia thurberi* and *T. rotundifolia* are further differentiated based on the nature of the peduncle and leaf margin.

These four groupings correspond well not only to the data derived from the evolutionary analyses, but also to the data resulting from the numerical taxonomic studies. Referring to Fig. 7, it is immediately evident that the two main groups formed in the phylogenetic reconstruction are the two main clusters formed in the numerical taxonomic analysis. Further, the subgroups are also supported. Only in the case of the relationships of *T. pedunculata* and *T. fruticosa* is there a discrepancy. The clustering level, however, is very low and not as powerful as their grouping based on an evolutionarily determined character trend. Based on the numerical taxonomic study and the phylogenetic reconstruction, the taxa within the subgeneric categories (La Duke, 1982) are (see Taxonomic Treatment for validation): Section *Tithonia:* Series *Tithonia (T. rotundifolia, T. tubaeformis, T. thurberi, T. brachypappa);* Series *Grandiflorae (T. diversifolia, T. koelzii);* Series *Fruticosae (T. fruticosa, T. pedunculata):* Section *Mirasolia (T. calva* [+ 2 vars.], *T. hondurensis, T. longiradiata).*

MORPHOLOGY AND TAXONOMIC CRITERIA

As a guide to the use of the keys and descriptions in *Tithonia,* details of the taxonomic value of morphological characters in the genus are given below.

Habit. Two basic types of habit appear within *Tithonia.* The first is herbaceous, with ascending stems in *T. brachypappa, T. rotundifolia, T. thurberi,* and *T. tubaeformis.* The second is the woody condition in the remainder of the genus. Variation occurs from weakly woody in *T. diversifolia, T. fruticosa,* and *T. koelzii,* to strongly woody shrubs such as *T. calva* and *T. pedunculata.*

Leaves. Leaf shape, base, and the presence or absence of a petiole are reliable characters in recognition of taxa. The most common leaf shape is linear-lanceolate, but variation ranges from linear in *Tithonia calva* var. *auriculata* to deltate in *T. tubaeformis* to 3-5 lobed in *T. diversifolia* and *T. rotundifolia.* Most taxa have sessile leaves, but four taxa are always petiolate: *T. koelzii, T. rotundifolia, T. thur-*

beri, and *T. tubaeformis*. Winged petioles are absent in *Tithonia*, but long leaf bases are present resulting in many sessile leaves. Leaf bases are either attenuate, auriculate, or decurrent. *Tithonia koelzii* and *T. diversifolia* have an unusual auricle at the base of the petiole. This condition is found in these species only when grown in mesic conditions, but the adaptive value is unknown.

Involucre. The phyllaries comprising the involucres are of two types. The spathulate type is the most common, with the linear or oblong type found in six taxa. The number of series of phyllaries ranges from 2 to 4 (5) and can be used in many taxa as a reliable character. In some taxa (e.g. *T. longiradiata*), the innermost series of phyllaries approaches the nature of pales. They are tan, striate, and have the characteristic paleaceous acuminate tip. In some taxa, the overall nature of the phyllaries is the best character for species recognition, but it is difficult to describe effectively.

Pales. The pales of taxa of *Tithonia* sort neatly into two types. Aristate-tipped loosely enclosing pales occur in Section *Tithonia*. In contrast, shorter, acute to infrequently aristate pales which tend to enclose the achenes tightly occur in section *Mirasolia*.

Florets. Few floret characters are useful in differentiating taxa. Most populations of *Tithonia rotundifolia* have orange ray florets, but the yellow condition typical of the other taxa of *Tithonia* also occurs in some populations. Anther color is black in the disk florets in most taxa except *T. calva* and *T. fruticosa*, which have tan or brown anthers. The shape of the disk floret varies very little and is not useful in delimiting taxa. Anther length is useful in recognizing some taxa, such as *T. calva* var. *calva* vs. *T. calva* var. *lancifolia*, but it varies considerably in others.

Achenes and Pappus. Shape of the achenes and nature of the pappus are important at the sectional and in some cases at the specific levels. Section *Mirasolia* is characterized by small (3–5 mm) rounded-quadrangular, black or mottled epappose achenes with eliasomes. Section *Tithonia* is characterized by larger (4.5–9 mm) quadrangular or triangular, black, brown, or mottled pappose achenes. The pappus is a basally and laterally fused squamellar ring with or without awns (Figs. 2 & 3). One taxon of this section, *T. pedunculata*, has, in addition to pappus, an eliasome at the base of the achene.

TAXONOMIC TREATMENT

Tithonia Desf. ex Juss.

Tithonia Desf. ex Juss. Gen. Pl. 189. 1789.

Tithonia Desf. ex Gmelin, Syst. Nat. **2:** 1259. 1791.

TYPE species: *Tithonia uniflora* Desf. ex Gmelin = *Tithonia rotundifolia* (Mill.) S. F. Blake.

Tithonia subgen. *Mirasolia* Sch.-Bip. in Seemann, Bot. Voyage Herald **305.** 1856. TYPE species: *Tithonia calva* Sch.-Bip in Seemann.

Mirasolia (Sch.-Bip. in Seemann) B. & H. Gen. Pl. **2:** 367. 1873.

Urbanisol O. Kuntze, Rev. Gen. Pl. **1:** 370. 1891.

Superfluous name, based on type of *Tithonia* Desf. ex Gmelin.

Erect, annual or perennial, herbs, shrubs, or trees. Stems terete, yellow, green, brown, or purple; glabrous to densely villous with hairs to 15 mm long. Leaves alternate (occasionally opposite below), petiolate or sessile; blades linear to deltate or 3–5 lobed, at apex acute to acuminate, at base attenuate to auriculate or decurrent, on upper surface pilose to subglabrous, on lower surface pilose to subglabrous, at margin serrate to crenate. Peduncle hollow-flared (fistulose), villous to pilose or subglabrous. Heads mostly solitary. Receptacle hemispheric to convex; pales stiff, striate, aristate to acuminate or acute, usually with two secondary lobes, embracing the achenes, persistent. Phyllaries 2–5 seriate, graduated, linear to broadly rounded, at apex acute to rounded, glabrous to pilose. Ray florets 8 to 30, neuter; ligules yellow or orange, pappus present or absent; achenes white to light tan, triangular. Disk florets hermaphrodite; corollas yellow, with lobes 5; anthers black, brown, or tan; styles bifid, at base usually swollen, with or without an ovarian disk[1]; stigmas pappillate; pappus absent or of fused squamellae and sometimes awns; achenes fertile, black, brown, or mottled, triangular, rounded-quadrangular to quadrangular; with or without eliasome at base. Chromosome number, $n = 17$. TYPE SPECIES: *Tithonia uniflora* Desf. ex Gmelin = *Tithonia rotundifolia* (Mill.) S. F. Blake.

KEY TO THE TAXA

1. Achenes of the disk florets all epappose ..... (2)
   2. Phyllaries linear to lanceolate, acute-tipped ..... (3)

[1]The structure encircles the style at the base on top of the ovary. It is probably a nectary, but it is not known if nectar is produced.

3. Leaves linear to linear-lanceolate, usually with one main vein, 8–12 times as long as broad ..... 9c. *T. calva* var. *auriculata*
3. Leaves ovate to lanceolate-ovate (sometimes linear-lanceolate) with main vein branching into three smaller veins about 1/3 of the way up from the base, less than 8 times as long as broad ..... (4)
4. Heads 7–9 mm diam; outer phyllaries 7 9 mm long; anthers 1.5–2 mm long..... 9b. *T. calva* var. *lancifolia*
4. Heads 10–14 mm diam; outer phyllaries 10–14 mm long; anthers 3.5 mm long ..... 9a. *T. calva* var. *calva*

2. Phyllaries oblong with broadened tips..... (5)
5. Leaves linear to linear-lanceolate with margin revolute, 0.5 2.8 cm wide; disk florets about 60 80 ..11. *T. hondurensis*
5. Leaves triangular to ovate to long-lanceolate, without strongly revolute margin, 2.6 13.5 cm wide; disk florets about 100 200..... 10. *T. longiradiata*

1. Achenes of at least some of the disk florets with pappus..... (6)
6. Leaves lanceolate to lanceolate-ovate, at margin entire to crenate..... (7)
. Phyllaries 3-seriate, linear; leaves hispid; occurring only in Oaxaca, Mexico ..... 8. *T. pedunculata*
7. Phyllaries 4-seriate, ovate; leaves soft-villous; occurring in northern Mexico..... 7. *T. fruticosa*
6. Leaves deltate, at margin entire to 3–5 lobed..... (8)
8. Leaf base strongly decurrent on stem..... 2. *T. brachypappa*
8. Leaf base attenuate or with only ephemeral auriculate lobes at base of petiole..... (9)
9. Phyllaries in 2 series..... 3. *T. tubaeformis*
9. Phyllaries in 3 4 series ..... (10)
10. Ligules of ray florets greater than 45 mm long..... (11)
11. Large shrub; leaves deltate and/or 3–5 lobed; phyllaries 4 (rarely 3) seriate; widespread in Mexico and Central America; disk florets 80–120 ..... 6. *T. diversifolia*
11. Small tree; leaves all deltate; phyllaries 3-seriate; endemic to Jalisco; disk florets 60 or less..... 5. *T. koelzii*
10. Ligules of ray florets less than 33 mm long ..... (12)
12. Ray florets orange (rarely yellow); ligules 20–33 mm

long, 6–17 mm wide; leaves deltate and/or 3–5 lobed, soft-pubescent, anthers 4–5.5 mm long..... .....1. *T. rotundifolia*

12. Ray florets yellow; ligules 9–15 mm long, 4–6 mm wide; leaves deltate, hispid; anthers 2–4 mm long... .....4. *T. thurberi*

I. *Tithonia* section *Tithonia*

Tithonia Desf. ex Juss. Gen. Pl. 189. 1789. TYPE SPECIES: *Tithonia uniflora* Gmelin = *Tithonia rotundifolia* (Mill.) S. F. Blake.

Shrubs or herbs; leaves lanceolate to deltate, sessile to petiolate, with margin serrate to 3–5 lobed; involucre 2–5 seriate; disk achenes quadrangular or triangular, pubescent, with pappus of fused squamellae, with or without awns, or nearly lacking in some achenes. Species 1–8.

1. Series *Tithonia*

Herbaceous annuals; leaves deltate to 3–5 lobed; involucre 2–3 seriate. Species 1–4. TYPE SPECIES: *Tithonia rotundifolia* (Mill.) S. F. Blake.

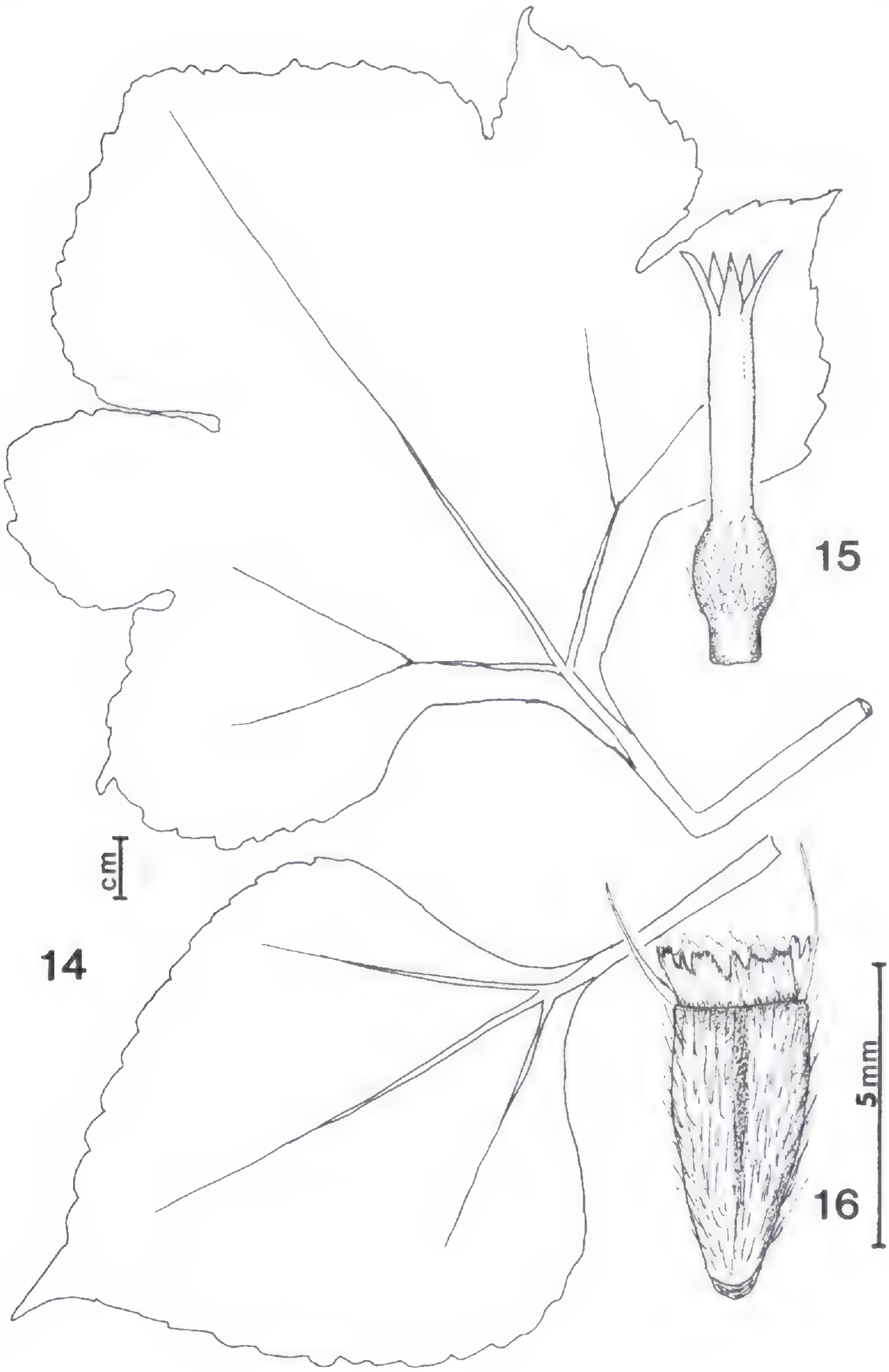
1. **Tithonia rotundifolia** (Miller) S. F. Blake, Contr. Gray Herb. ser. **52:** 41. 1917 Figs. 14–16.

Tagetes rotundifolia Miller, Gard. Dict. ed. **8.** *Tagetes* #4. 1768. TYPE: MEXICO, Veracruz, grown from seed, probably at the Chelsea garden, *W. Houstoun s.n.* (HOLOTYPE, BM! [photo, GH!, NY!, OS!, UC!]).

Tithonia uniflora Desf ex Gmelin, Syst. Nat. ed. 1791, *t.2.* 1259. 1791. TYPE: location, date, and collector unknown. (HOLOTYPE, not located). The location of J. F. Gmelin's herbarium is unknown (Stafleu & Cowan, 1976).

Tithonia tagetiflora Lamarck, Tabl. Ency. Metd. **2:** 284, *t. 708.* 1797. TYPE: location, date and collector unknown (HOLOTYPE, the illustration is taken as the type). Although J. B. Lamarck's herbarium is housed at Paris (P-LA), no specimen has been located.

Tithonia tagetiflora Desf. Ann. Mus. Natl. Hist. **1:** 49. *pl. 4.* 1802. TYPE: specific locality unknown, date unknown, *Thiery s.n.* (HOLOTYPE, P [photo GEND!, OS!]).



Figures **14–16.** Leaf outlines (Fig. **14**; *La Duke et al. 510a*, OS), disk corolla (Fig. **15**), disk achene (Fig. **16**) of *Tithonia rotundifolia*. Figures 15 and 16, *La Duke et al. 480*, OS; same scale.

Helianthus speciosus Hook. Curtis Bot. Mag. ser. 2. **3:** *t. 3295.* 1834. TYPE: location, date and collector unknown (HOLOTYPE, K! [photo, GH!, NA!, OS!]).
Leighia? speciosa (Hook.) DC. Prodr. 5: 583. 1836.
Tithonia aristata Örsted, Natur. For. Kjob. Vid. Medd. **1852:** 114. 1852. TYPE: COSTA RICA, Aguacate, No date *A. S. Örsted s.n.* (HOLOTYPE, specimen not found, drawings of presumed holotype at C!). The handwriting on the drawing at C is that of Örsted and the drawing matches well with the description.
Tithonia heterophylla Griseb. Bonplandia **6:** 9. 1858. TYPE: PANAMA, specific locality unknown, 1810, *E. P. Duchassaing s.n.* (HOLOTYPE, GOET! [photo, OS!]; ISOTYPE, GOET! [photo, OS!]).
Tithonia speciosa (Hook.) Griseb. Cat. Pl. Cub. 155. 1866.
Tithonia macrophylla S. Wats. Proc. Amer. Acad. Arts. **26:** 140. 1891. TYPE: MEXICO. Jalisco, Barranca near Guadalajara, Sept 1889, C. G. *Pringle 2798* (HOLOTYPE, US!; ISOTYPES, F!, GH!, MICH!, NY!, US!).
Urbanisol tagetfolius var. *normalis* O. Kuntze, Rev. Gen. Pl. **1:** 370. 1891. TYPE: Location, date, and collector unknown (HOLOTYPE, not located).
Urbanisol tagetifolius var. *speciosus* O. Kuntze, Rev. Gen. Pl. **1:** 370. 1891. TYPE: location, date, and collector unknown (Holotype, not located).
Urbanisol aristatus (Örsted) O. Kuntze, Rev. Gen. Pl. **1:** 371. 1891.
Urbanisol heterophyllus (Griseb.) O. Kuntze, Rev. Gen. Pl. **1:** 371. 1891.
Tithonia speciosa (Hook.) Klatt in Durand & Pittier, Ext. Bull. Soc. Roy. Bot. Belg. **31:** 203. 1893. Invalid name, later homonym.
Tithonia vilmoriniana Pampanini, Bull. Soc. Bot. Ital. **1908:** 133. 1908. TYPE: MEXICO, Michoacan, Jacona, *Collector unknown s.n.* (HOLOTYPE, FI!).

Erect, annual, herbaceous, 1–4 m tall. Stems round, green to tan to purple, glabrous to softly pubescent. Leaves alternate with petioles 2–10 cm long; blades deltate to triangular to 3–5 lobed, 9–38 cm long, 4–30 cm wide, at apex acute to acuminate, at base attenuate, on upper surface glabrous to hispid, on lower surface sparsely pubescent to villous, at margin crenate to serrate. Peduncles 11–27 cm long, 3–10 mm diam, short-villous to to glabrous near head. Heads usually solitary, heterogamous. Receptacle 7–13 mm diam. Phyllaries 14–21, (two) three-seriate, graduated, linear to lanceolate; outer bracts 17–30 mm long, 4–7.5 mm wide, at apex acute, dense minute pubescence on abaxial surface; inner bracts 16–28 mm long, 5–8 mm wide, at apex acute to rounded, dense minute pubescence on abaxial surface. Pales striate, 11.5–15 mm long, 2–3 mm wide, apex acuminate to aristate, 2.5–5.5 mm long, usually with secondary lobes, occasionally minutely pubescent on tip. Ray florets 8–13; ligules usually orange, sometimes yellow, oval to oblong, 20–33 mm long, 6–17 mm wide, at apex trifid; tube 1.5–2.5 mm long, 0.75–1 mm diam, pappus absent or short scales or awns; achenes one-seriate, triangular, white-tan, sterile. Disk florets about 60–90; corollas yel-

low; corolla lobes 5, 1 mm long, 0.5 mm wide, at apex acute; throat cylindrical with expanded minutely pubescent base, with cylindrical portion 3.5–5 mm long, 1–1.5 mm diam, with expanded portion 1–2 mm long, 1–2 mm diam; tube minutely pubescent, 0.5–1.25 mm long, 0.5–1 mm diam; anthers black, 4–5.5 mm long; styles 7–10 mm long; stigmas pappillate, 2 3.5 mm long; pappus fused squamellae with 2 awns; achenes fertile, quadrangular, black, brown, or mottled, pubescent, 5–7 mm long, 1.5–2.5 mm diam, at base smooth without eliasome. Chromosome number $n = 17$.

PRINCIPAL FLOWERING TIME: November — January.

DISTRIBUTION: Tropical forests or open areas throughout central and southern Mexico, south to Panama (Fig. 17). Introduced worldwide and escaped.

Tithonia rotundifolia is the type species of the genus. The plants are widespread throughout most of Mexico and Central America. Populations with orange rays are typical but yellow-rayed populations exist *(La Duke et al. 520 & 529),* mostly in Central America.

This taxon has been often confused with *Tithonia diversifolia,* from which it differs in many features. *Tithonia rotundifolia* is an annual, with linear-lanceolate phyllaries in (two-) three series and ray ligules 20–33 mm long, whereas *T. diversifolia* is a herbaceous perennial, with lanceolate to broadly ovate phyllaries in (three-) four series, and ray ligules 48–69 mm long. These taxa often are confused due to the similarity of the 3–5 lobed leaves. Recently the embryology of this taxon was described (Pullaiah, 1978) but no comparisons with other taxa of *Tithonia* were included.

REPRESENTATIVE SPECIMENS. ARGENTINA. **Jujuy:** Huaico, *Cabrera et al. 23594* (F). BELIZE. **Cayo:** El Cayo, *Bartlett 12099* (F, GH, LL, MICH, NA, US). CHINA. **Kiangsu:** Nanking, *Chiao 12955* (C, UC). COSTA RICA. **Alajuela:** 5 10 mi W of Naranjo on rte ca-1, *Stuessy & Gardner 4452* (OS); on freeway near Grecia, *Stuessy & Gardner 4468* (OS); ca 15 mi S of La Marina, then to Balneario Agua Caliente, *Stuessy & Gardner 4467* (OS). **Puntarenas:** 35.1 mi SE of San Isidro del General on rte 2 (ca-1), *Stuessy & Gardner 4505* (OS). CUBA. **Havana:** Vento, *Wilson 1325* (F, GH, NY, POM, US). EL SALVADOR. **Ahuachapán:** 5 mi SE of Hachadura (Guatemala border) on rte ca-2, *Stuessy & Gardner* 4565 (OS). **La Libertad:** ca 13 mi W of La Libertad on rte ca-2, *Stuessy & Gardner 4564**[1] (OS). **San Miguél:** 24.3 mi E of El Transito on rte ca-2. *Stuessy & Gardner* 4562 (OS). **Sonsonate:** vicinity of Izalco, *Pittier 1976* (F, US). GUATEMALA. **Chiquimula:** just W of town of Concepción Las Minas, at bridge over rte 20, *Stuessy & Gardner 4373* (OS). **Escuintla:** .1 mi N of intersection to El Naranjo on ca-9, *La Duke et al. 528* (OS); 4.8 mi S of intersection of ca-9 & ca-2 on ca-9, *La*

[1]Asterisk indicates chromosome voucher.

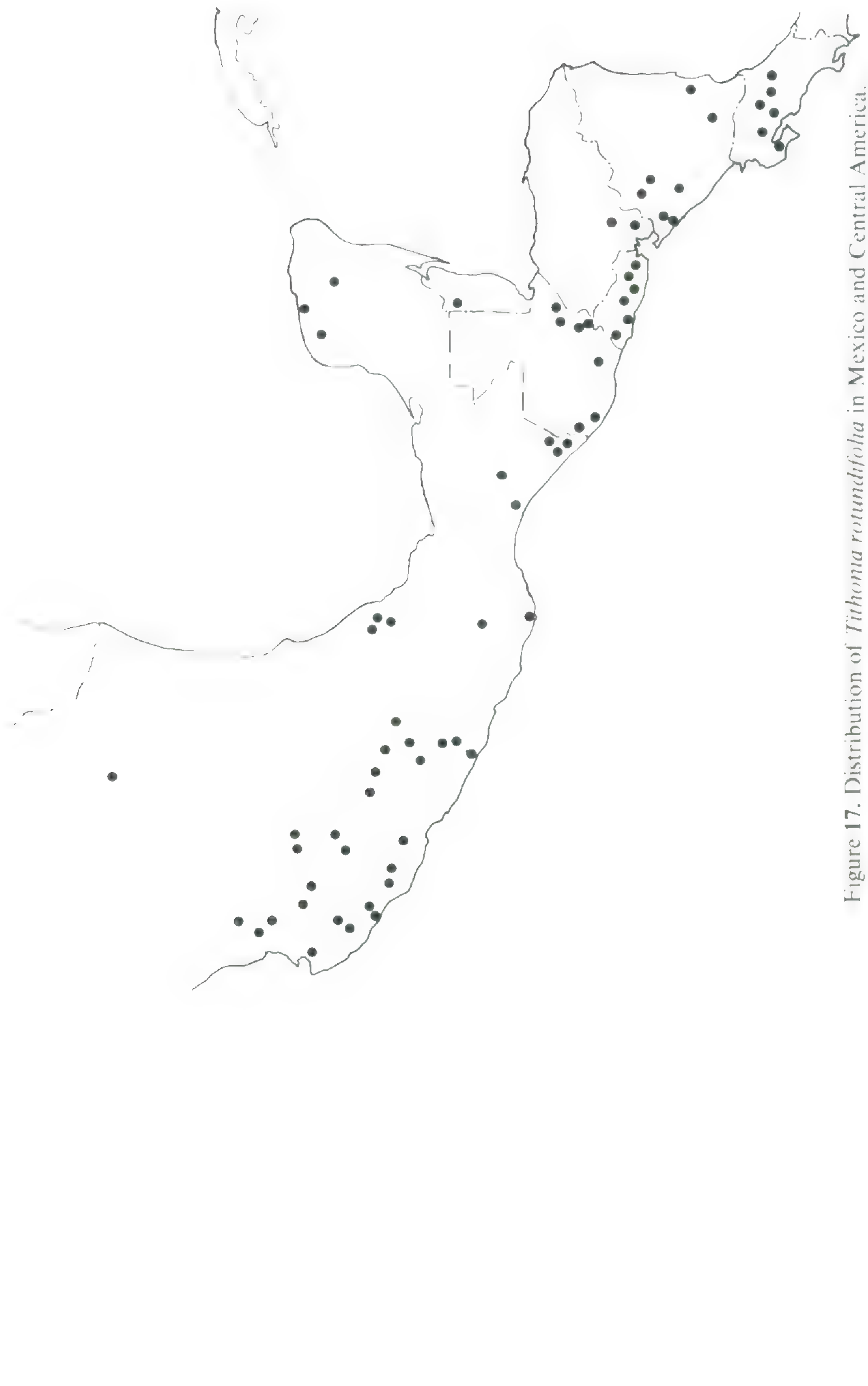


Figure 17. Distribution of *Tilhonia rotundifolia* in Mexico and Central America.

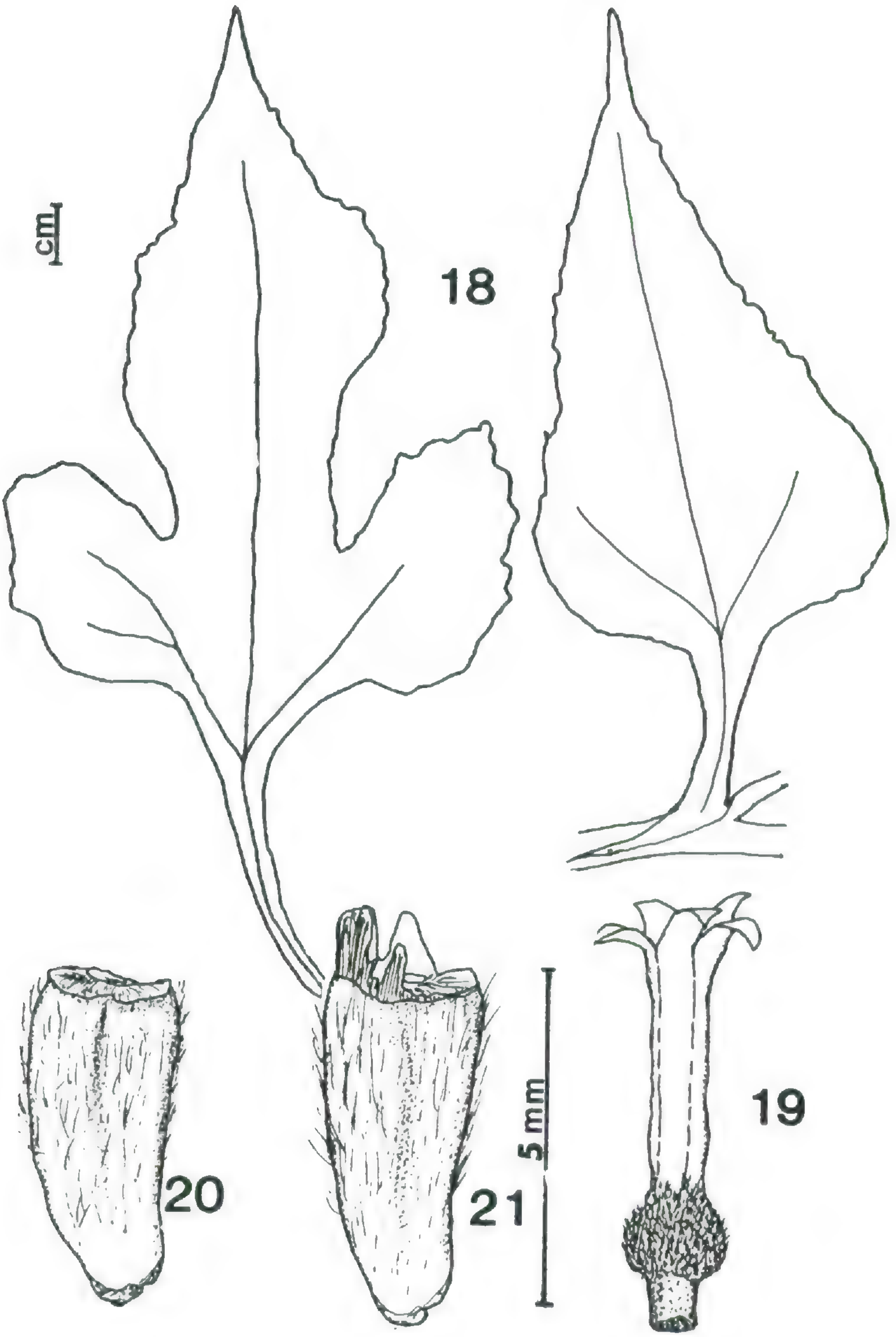
*Duke et al. 529** (OS). **Retalhuleu:** in coffee plantation of Mulua, *Molina 26971* (F, MICH). **San Marcos:** 2.3 mi S jct rd to Malacatán on rte ca-2, *Stuessy & Gardner 4569** (OS). **Zacapa;** Gualán, *Kellerman 5329* (F, OS). HONDURAS. **Comayagua:** ca 15 mi SE of Siguatepeque on rte 1, *Stuessy & Gardner 4417* (OS).

MÉXICO. **Chiapas:** 13 km N of Arriaga along Mex hwy 195, *Breedlove 19855* (OS, MEXU, MICH); Saltillo, *Palmer 558* (GH, K, MO, NY, US). **Colima:** 5 k W of Tecomán just S of intersection of 110 on 200, *La Duke et al. 392** (OS). **Guerrero:** Acapulco & vicinity, *Palmer 631* (OS, F, GH, K, MICH, MO, NY, UC, US); SE edge of Cacahuamilda on Rte 55 toward Taxco, *Stuessy & Gardner 4204** (OS). **Jalisco:** barranca of Tequila, *Pringle 4601* (F, GH, MO, NY, UC, US); W limits of Jalostotitlán on rte 80, *Stuessy & Gardner 4093* (OS); 3 5 mi S of Puerto Vallarta on rd to Tomatlán, *Stuessy & Gardner 4132** (OS); ca 6 mi N of La Resolana (Casimiro Castillo) on rte 80, *Stuessy & Gardner 4135** (OS). **México:** Temascaltepec, *Hinton 1992* (OS, K, MO, NY, US). **Michoacán:** Coalcomán, *Hinton 12452* (GH, K, LL, MICH, NY, UC, US); .7 mi E of rd to Chavinda on hwy 15, S side of rd; *La Duke et al. 393** (OS); 1.9 mi W of Rd to Gómez Farias on hwy 15, *La Duke et al. 480* (OS). **Nayarit:** above La Laguna, a crater lake near Santa Maria del Oro & 30 mi SE of Tepic, *Cronquist 9597* (GH, MICH, MO, NY, TEX, US). **Oaxaca:** 1.7 mi W of Oaxaca-Chiapas line on rte 190, *La Duke et al. 510A** (OS). **Veracruz:** puente nacional, *Arreguín 2643* (DS, ENCB, F, MICH, NY, TEX). **Yucatán:** Kancabconot, *Gaumer 23524* (C, F, GH, MO, POM, US); Mérida, *Souze 6* (NA).

NICARAGUA. **Granada:** Lake Nicaragua, *Hamblett 1114* (F, GH, MO, NY, SMU, UC). **León:** in open field rt 26 Telica, *Hamblett et al. 210* (F, GH, MICH, MO, NY, SMU, UC). **Madriz:** ca 5 mi E of Honduras-Nicaragua border on rte 1, *Stuessy & Gardner 4436* (OS). **Managua:** rt 1 Tipitapa, *Seymour 2347* (DUKE, GH, MO, NY, SMU, UC). **Zelaya:** in open pasture Bluefields, *Zelaya 447* (F, GH, MO, SMU, UC). NIGERIA. 1 km S Oyo, rd. to Ibadan, Bida, *Bruner 427* (OS). PANAMÁ. Taboga Island, *Celestino 41* (US). RHODESIA. Que Que railway, *Biegel 1043* (K). SAN DOMINGO. without locality, *Wright et al. 267* (US). SAN SALVADOR. Republic of Salvador, *Velasco 8869* (GH, US). UNITED STATES. **Florida:** Tallahassee, *Kral 3739* (FSU, GH). VENEZUELA. **Distrito Federal:** around Caacas, *Pittier 7435* (GH, US). WEST INDIES. HAITI: Haiti, *Ekman 7197* (F, GH, K).

2. **Tithonia brachypappa** Robins. Proc. Amer. Acad. Arts **27:** 174. 1892. TYPE: MÉXICO, San Luís Potosí, Las Palmas, 15 Oct 1890, *C. G. Pringle 3675* (LECTOTYPE, GH!; ISOLECTOTYPES, F (FRAG)!). Figures 18–21.

Erect, annual, herbaceous, 2–3 m tall. Stems round, red to brown to tan, subglabrate to sparsely pilose. Leaves alternate, sessile; blades triangular to 3–5 lobed, 11–21 cm long, 3–11.5 cm wide, at apex acuminate, at base attenuate, auriculate-decurrent on stem, on upper and lower surfaces hispid, at margin serrate. Peduncles 10–30 cm long, 4 7 mm diam, hispid-pilose near head, becoming glabrate below. Heads usually solitary, heterogamous. Receptacle 8 9 mm diam. Phyllaries 15 19, three-seriate, graduated, linear to spathulate; outer bracts 5–9 mm long, 2 3.5 mm wide, at apex



Figures **18–21.** Leaf outlines (**18**; unlobed leaf, *Stuessy and Gardner 4038,* OS, lobed leaf, *Crutchfield and Johnston 5727,* TEX); disk corolla (**19**), outermost disk achene (**20**), and inner disk achene (**21**) of *Tithonia brachypappa.* Figures 19–21, *La Duke and Jansen 418,* OS; same scale.

round with acute tip, minutely pubescent on abaxial surface; inner bracts 12–16 mm long, 4.5–9 mm wide, at apex rounded, minutely pubescent on abaxial surface. Pales striate, 8–12 mm long, 2–2.5 mm wide; apex aristate, 2–5 mm long, usually with lateral lobes. Ray florets 7–8; ligules yellow to orange-yellow, linear, 15–25 mm long, 4–8 mm wide, at apex trifid; tube 1.5 mm long, 0.75–1 mm diam; pappus absent; achenes one-seriate, white to yellow, triangular, sterile. Disk florets 47–70; corollas yellow; corolla lobes 5, 0.75–1 mm long, 0.5–.75 mm wide, at the apex acute; throat cylindrical with expanded minutely pubescent base, with cylindrical portion 3–5 mm long, 0.75–1 mm diam, with expanded portion 1 mm long, 1–1.5 mm diam; tube minutely pubescent, 0.75–1 mm long, 0.5–.75 mm diam; anthers black, 4.5 mm long; styles 7–8.5 mm long; stigmas papillate, 2–3 mm long; pappus lacking on some achenes, fused squamellae on most; achenes fertile, black, brown, or mottled, 4.5–6 mm long, 2–2.5 mm diam, at base (without eliasome). Chromosome number $n = 17$.

PRINCIPAL FLOWERING TIME: September-November (April).
DISTRIBUTION: Tamalipas and San Luis Potosí, Mexico (Fig. 22).

This species can be easily recognized by the decurrent leaf bases. As noted by Blake (1921), the achenes show variation in pappus. The disk achenes on the outside of the head usually have very little, if any, pappus (Fig. 19), but the amount of pappus increased toward the center of the head (Fig. 20). The adaptive significance of this variation is not known.

This taxon is most closely related to *T. rotundifolia* and differs in the following critical characters: 1) pappus of squamellae vs. awns plus squamellae, 2) sessile leaves, with decurrent leaf bases vs. petiolate leaves with attenuate leaf bases, and 3) spathulate phyllaries vs. linear to oblong phyllaries.

REPRESENTATIVE SPECIMENS. MÉXICO. **San Luís Potosí:** limestone hills, Las Palmas, *Pringle 6143* (BM, BR, K, S, UC, US); 10–20 mi W of Ciudad Valles on rte 86, *Stuessy & Gardner 4038* (OS); 2.2 mi E of intersection to El Salto on rte 80, *La Duke et al. 587** (OS). **Tamaulipas:** 6 mi N of Aldama on rd. to Soto La Marina, *Crutchfield & Johnston 5727* (MICH, TEX); .1 mi N of Santa Fé on Hwy 85, *La Duke & Jansen 418** (OS); 40–60 mi S of Ciudad Victoria on rte 101, *Stuessy & Gardner 4033** (OS).

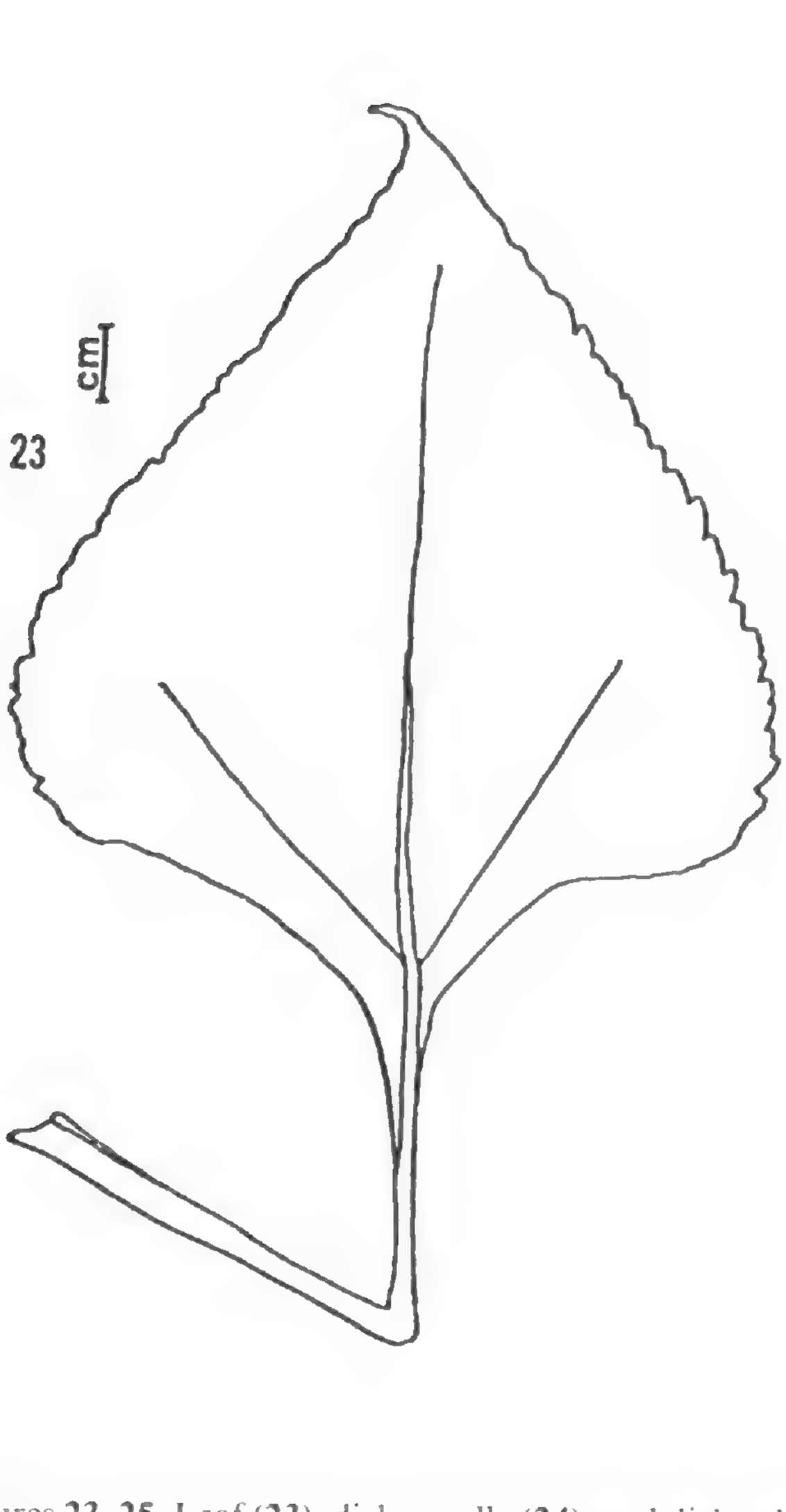
Figure 22. Distribution in Mexico and adjacent United States of *Tithonia koelzii* (closed triangles), *T. brachypappa* (dots), *T. calva* var. *calva* (circles), *T. calva* var. *lancifolia* (open triangles), *T. calva* var. *auriculata* (closed squares), *T. fruticosa* (asterisks), and *T. thurberi* (open squares).

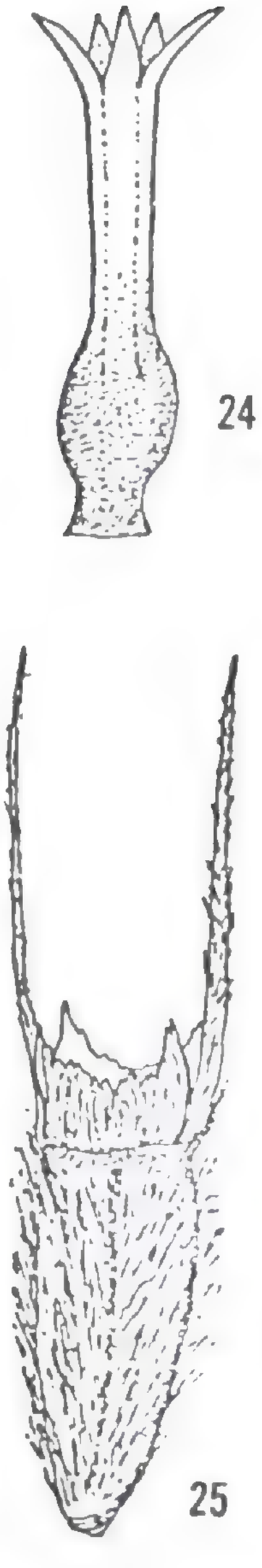
3. **Tithonia tubaeformis** (Jacq.) Cass. Dict. Sci. Nat. **35:** 278. 1825. Figs. 23–25.

Helianthus tubaeformis Jacq. Pl. Hort. Schonbr. **3:** 65. *pl. 375.* 1798. TYPE: MEXICO, "sub dio floret autumno" (HOLOTYPE, the illustration is taken as the type). Loans were requested from institutions (AWH, BM, CGE, LIV, OXF, and UPS) where Jacquin specimens are known to be (D'Arcy, 1970), but no specimen has been located.

Helianthus tubaeformis Ortega, Nov. Rar. Pl. Horti. Reg. Botan. Matrit. dec. 8. 101. 1798. TYPE: "Nova Hispanae", Flowers in Oct-Nov, *D. de la Cal s.n.* (LECTOTYPE here chosen, M! [photo, OS!]).

Tithonia helianthoides Bernh. Gart. Mag. **2:** 156. *pl. 15.* 1826. TYPE: location, date and collector unknown (HOLOTYPE, the illustration is taken as the type).





Figures **23–25.** Leaf (**23**), disk corolla (**24**), and disk achenes (**25**) of *T. tubaeformis* (*La Duke et al. 406*, OS). Figs. 24 and 25 same scale.

Urbanisol tubiformis (Cass.) Kuntze, Rev. Gen. Pl. **1:** 371. 1891.
Tithonia tubaeformis var. *bourgaena* Pampanini, Bull. Soc. Bot. Ital. **1908:** 134. 1908. TYPE: MEXICO, Valley of Cordoba, 20 Dec 1865-1866, *E. Bourgeau 1566* (HOLOTYPE, FI! [photo OS!]).

Erect, annual, herbaceous, 1–3 m tall. Stems round, red to yellow to tan to brown, moderately to densely pubescent. Leaves alternate with petioles 2–11 cm long; blades deltate, 5–25 cm long, 6–17 cm wide, at apex acuminate, at base attenuate, on upper surface strigose-hirsute, on lower surface hirsute to villous, at margin cre-

nate to serrate. Peduncles 10–45 cm long, 4–12 mm diam, moderately to densely pubescent. Heads usually solitary, heterogamous. Receptacle 8–25 mm diam. Phyllaries 15–25, two-seriate, graduated, linear to oblong (oblanceolate); outer bracts 15–30 mm long, 2–5 mm wide, at apex acute, on abaxial surface moderately pubescent; inner bracts 14–24 mm long, 3–4 mm wide, at apex acute, abaxial surface minutely pubescent. Pales striate, tan to purple, 10–18 mm long, 2–3.5 mm wide; apex acuminate to aristate, 3–9 mm long, usually with lateral lobes, minutely pubescent above. Ray florets 11–18; ligules yellow, oblong to ovate, 14–45 mm long, 5–15 mm wide, at apex trifid; tube 1.5–3 mm long, 0.75–1 mm diam; pappus absent or short scales; achenes one-seriate, triangular, white-tan, sterile. Disk florets (30–) 90–120; corollas yellow; corolla lobes 5, 1 mm long, 0.5 mm wide, at apex acute; throat cylindrical with expanded minutely pubescent base, with cylindrical portion 3–5 mm long, 1–2 mm diam, with expanded portion 1–2 mm long, 1–2 mm diam; tube minutely pubescent, 0.25–1 mm long, 0.5–.75 mm diam; anthers black, (4–) 5 mm long; styles 4.5–9 mm long; stigmas papillate, 1–3 mm long; pappus of fused squamellae with or without two awns; achenes fertile, brown, black, or mottled, pubescent, quadrangular, 4–6 mm long, 1.75–3 mm diam, smooth at base without an eliasome. Chromosome number $n = 17$.

PRINCIPAL FLOWERING TIME: August-November.

DISTRIBUTION: Weedy habitats throughout most of tropical Mexico, south to Panama (Fig. 26).

Tithonia tubaeformis is a weedy annual occurring throughout most of Mexico and Central America, often in cultivated or fallow fields. It is quite variable morphologically, but easily recognized by the linear, pubescent phyllaries, deltate leaves, and large annual habit. *Tithonia tubaeformis* hybridizes with *T. rotundifolia* in the field to produce F_1 hybrids with intermediate morphology and low fertility (see cytology section).

Tithonia tubaeformis is most closely related to *T. thurberi*, but is not known to be sympatric with it. *Tithonia tubaeformis* differs in possessing the following characters: 1) greater number of disk florets, 2) larger habit, 3) linear phyllaries vs. oblong to ovate phyllaries, and 4) a more widespread distribution (Fig. 22 vs. 26).

Figure **26.** Distribution of *Tithonia tubaeformis* in Mexico and Central America.

REPRESENTATIVE SPECIMENS. GUATEMALA. **Chiquimula:** dry thickets and pine forest btwn Jocotán and Camotán, *Molina 25216* (C, F, NY, US). **Huehuetenango:** on the ruins of Zaculen, *Skutch 1593* (F, GH, LL); 4 5 mi S Huehuetenango, rte ca-1, *Stuessy & Gardner 4325** (OS). **Jutiapa:** btwn Jutiapa and La Calera SE of Jutiapa, *Standley 76071* (F). **Sacatepequez:** 4 mi E El Tajar on rte ca-1, *La Duke et al. 533* (OS). **Santa Rosa:** Chupadero, *Heyde 4202* (F, GH, K, NY, US). MÉXICO. **Chiapas:** S of center of Amatenango del Valle, Municipio of Amatenango del Valle, *Ton 1066* (DS, DUKE, ENCB, F, MICH, NY). **Chihuahua:** NW of Chihuahua, *Lesueue 348* (ARIZ, F, GH, MO, TEX); Parral and vicinity 10 mi SE, *Gentry 17916* (LL, US). **Colima:** without locality, *Palmer 1220* (MICH, MO, NY, UC, US). **Distrito Federal:** Ciudad de México, *Arvizu 87* (ENCB). **Durango:** city of Durango and vicinity, *Palmer 690* (C, F, GH, K, MO, NY, UC, US); 9.2 mi SW Francisco I Madero on hwy 40, *La Duke et al. 380** (OS); .9 mi W of Leo Guzmán on hwy 40, *La Duke et al. 372A* (OS). **Hidalgo:** 2.6 mi S Trancas on rte 86, *La Duke et al. 580A* (OS). **Jalisco:** W limits of Jalostotitlán on rte 80, *Stuessy & Gardner 4094** (OS); ca. 5 mi NW Tequila on rte 15, *Stuessy & Gardner 4101** (OS); ca 26 mi NW Tequila on rte 15, *Stuessy & Gardner 4108** (OS); 1 mi N rd to Teocitatlán on hwy 33, *La Duke et al. 472** (OS). **México:** .3 mi W Tlapizahuac, *La Duke & Jansen 398** (OS); .5 mi S of Tenancingo on rte 55, *Stuessy & Gardner 4195** (OS). **Michoa-**

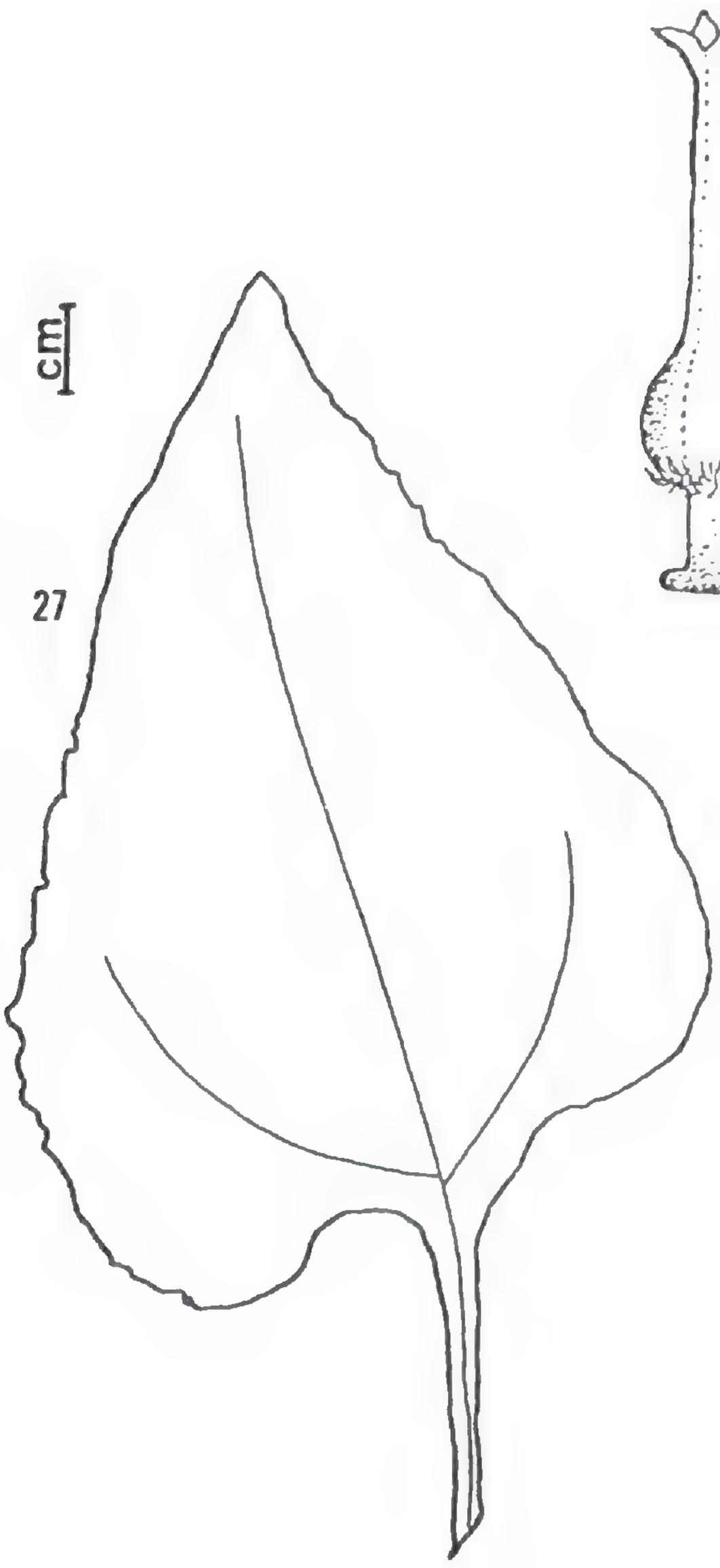
cán: Sierra Torricillas Coalcomán, *Hinton 12358* (GH, LL, MICH, NY, UC, US); 1.9 mi W of rd to Gómez Farías on hwy 15, *La Duke et al. 481** (OS). **Morelos:** valley Jojutla, *Pringle 9306* (F, GH, LL, MICH, NY, SMU, TEX, US, YU). **Nayarit:** Tepic, *Palmer 1851* (F, GH, NY, US); .6 mi S of hwy 15 & rd to Uzeta, *La Duke et al. 390** (OS). **Oaxaca:** .1 mi E of rd to Chivala on hwy 185, *La Duke & Jansen 406** (OS); 3.9 mi E of rd to La Mata on hwy 185, *La Duke & Jansen 407** (OS); between Huajuapán de León & Yanhuitlan, *Stuessy & Gardner 4249** (OS); 1 mi W Las Minas on rte 190, *La Duke et al. 509** (OS); 1.7 mi W Oaxaca-Chiapas border on rte 190, *La Duke et al. 511** (OS). **Puebla:** along rt 115 just SE of Morelos-Puebla border, *King 2920* (DS, MICH, NY, TEX, UC, US); 2.0 mi NE of rte 150 on rte 125, *La Duke et al. 570** (OS). **San Luís Potosí:** near Arriaga on rte 80, *Stuessy & Gardner 4075* (OS). **Sinaloa:** .3 mi W El Zapotillo on rte 40, *La Duke et al. 429* (OS). **Tamaulipas:** near San Vicente, *Von Rozynski 201* (F, MICH, NY). **Veracruz:** El Marzo, NW of Santa Ana Atzacán, *Rosas 271* (DS, GH, LL, MICH, MO).

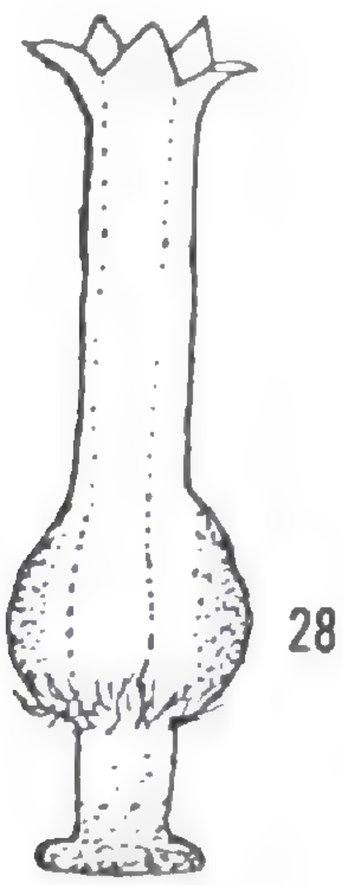
4. **Tithonia thurberi** A. Gray, Proc. Amer. Acad. Arts **8:** 655. 1873. TYPE: MÉXICO, Sonora, Magdalena, Oct 1851, *G. Thurber 910* (HOLOTYPE, GH!; ISOTYPES, GH!, K, [photo, OS!], MO!, NY!). Figs. 27–29.

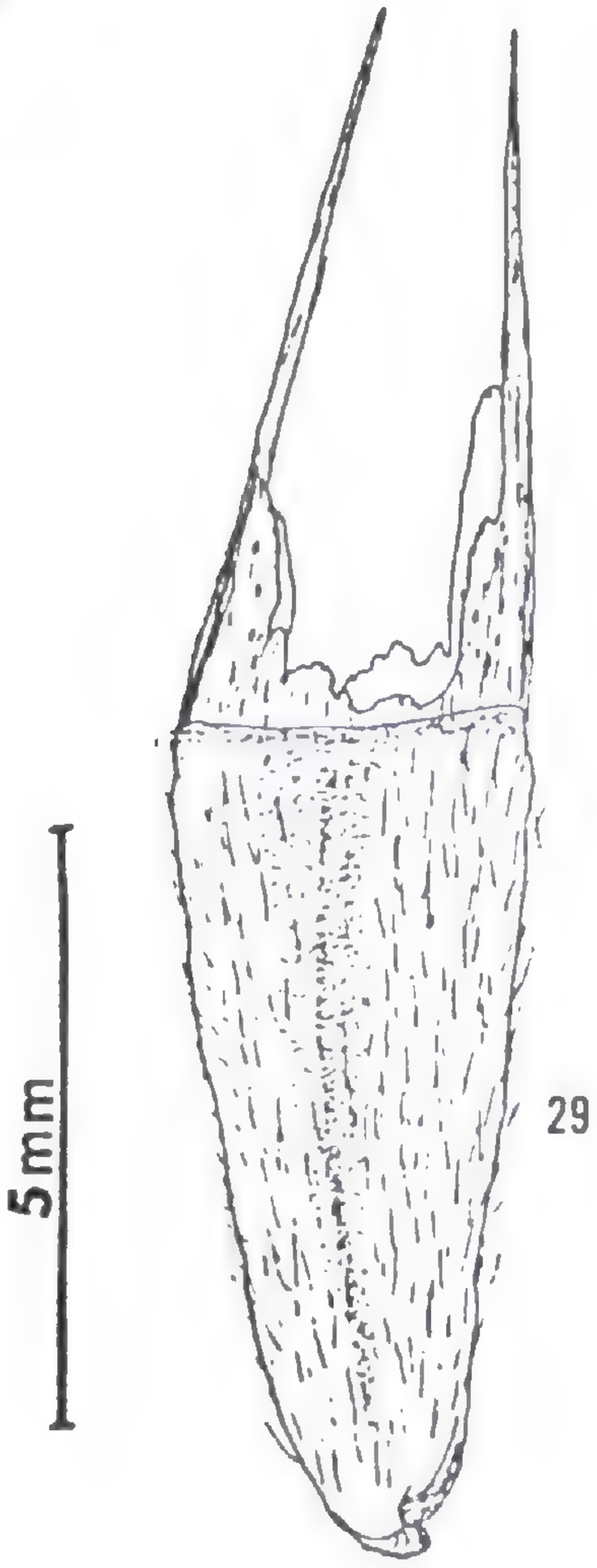
Tithonia palmeri Rose, Contr. U.S. Nat. Herb. **1:** 104. 1891. TYPE: MEXICO, Sonora, along watercourses and in canyons, Alamos, Sept 1890, *E. Palmer 721* (LECTOTYPE here chosen, US!; ISOLECTOTYPES, DS!, F!, GH!, K [photo, OS!], NY!, UC!, US!).

Urbanisol thurberi (A. Gray) Kuntze, Rev. Gen. Pl. **1:** 371. 1891.

Erect, annual, herbaceous, 0.7–2 m tall. Stems round, tan, glabrous to hirsute. Leaves alternate, with petioles 33 mm long or sessile; blades deltate, 7 28 cm long, 5.5–21.5 cm wide, at apex acuminate, at base attenuate, on upper surface sparsely hirsute, on lower surface hirsute with larger hairs on veins, at margin serrate. Peduncles 17 36 cm long, 3.5 6 mm diam, sparsely to moderately pubescent near the head. Heads solitary, heterogamous. Receptacle 7 11 mm diam. Phyllaries 13 16, three-seriate, slightly graduated, linear to spathulate; outer bracts 8–15 mm long, 2.5–4.5 mm wide, at apex acute, on abaxial surface minutely pubescent; inner bracts 12–15.5 mm long, 3.5 7 mm wide, at the apex acute, on abaxial surface glabrous. Pales striate, 11 16.5 mm long, 2 4 mm wide; apex acuminate, 3 mm long, usually with lateral lobes, glabrous. Ray florets 7 10; ligules yellow, oblong, 9 15 mm long, 4 6 mm wide, at apex trifid; tube 0.75–1.5 mm long, 0.5–.75 mm diam; pappus absent; achenes one-seriate, triangular, white-tan, sterile. Disk florets 40 60; corollas yellow; corolla lobes 5, 0.75 1 mm long, 0.5 .75 mm wide, at the apex acute; throat cylindrical with expanded minutely







Figures **27–29.** Leaf (**27**), disk corolla (**28**), and disk achene (**29**) of *Tithonia thurberi (Gentry 1830,* LL). Figures 28 and 29 same scale.

pubescent base, with cylindrical portion 3–4 mm long, 1–1.5 mm diam, with expanded portion 1–1.5 mm long, 1.2–2 mm diam; tube minutely pubescent, 1–1.75 mm long, 0.5–.6 mm diam, thickened; anthers black (brown), 2–4 mm long; styles 4–7.5 mm long; stigmas pappillate, truncate, 0.75–1.5 mm long; pappus laterally fused squamellae and two awns; achenes fertile, triangular (or quadrangular), 6–9 mm long, 1.75–3 mm diam, smooth at base without eliasome. Chromosome number, $n = 17$.

PRINCIPAL FLOWERING TIME: August-September (dependent on local rainfall).

DISTRIBUTION: Confined to xeric northern Sonora, Mexico and southern Arizona, U.S.A. (Fig. 17).

Tithonia thurberi, an annual, is one of the smaller taxa. It is limited in distribution and distinctive in its long pubescence on the veins of the leaves and broad pales enclosing long (6–9 mm) achenes.

REPRESENTATIVE SPECIMENS. MÉXICO. **Chihuahua:** Guasaremos, Río Mayo, *Gentry 1830* (ARIZ, F, GH, K, LL, MEXU, MO, NA, NY, UC, US). **Sonora:** on rd from Libertad to Datil, 8.6 mi from Serna-Libertad fork, *Wiggins 6100A* (DS); 31 mi S of Nogales, *Shreve 6607* (F); 31 mi S of Nogales, along Río de Los Alisos, *Wiggins 7023* (ARIZ, DS); open park-like flat 10 mi S of Santa Ana, *Wiggins & Reed 7203* (DS, MO, TEX, US); canyon of Agua Amarga, *White 3645* (ARIZ, GH, MICH); Horconcitos, Río Huachinera, *White 3717* (GH, MICH); 19 mi N of Colorado on rd to Mazatlán, *Wiggins 357* (DS, GH, MICH, MO, NA, NY, US); Benjamin Hill, *Gentry 17859* (LL, US); ca 4 mi E of Álamos along rd to Milpillas, *Henrickson 2429B* (RSA); La Pasión, 15 km NE of Tubutama, *Arizpa 99* (ENCB); 2 mi N of Los Janos on hwy 15, *La Duke et al. 421** (OS). UNITED STATES. **Arizona:** Helvetia, *Thornber 7226* (ARIZ, SMU); Baboquivari Canyon, *Peebles et al. 411* (ARIZ); Tumacacori Mission, *Peebles & Harrison 4666* (ARIZ, NA); Baboquivari Mtns, *Jones 25121* (DS, GH, LL, NA, POM, TEX, UC); Toro Canyon, Baboquivari Mtns, *Gilman 51* (ARIZ, DS, GH, NA); Toro Canyon, *Kearney & Peebles 10455* (ARIZ, LL, POM); 5 mi SW of Patagonia, *Benson 10414* (ARIZ); 7 mi W of US 89 toward Ruby, *Barr 68-S74* (ARIZ); just W of I 19 on AZ rte 289, *Keil & Pinkava K11095* (LL, OS); ca 5 mi NE of Nogales along a local rd just off hwy 82, *Urbatsch 2848* (OS).

2. Series *Grandiflorae* La Duke. Rhodora **84**:140. 1982.

Plant perennial shrubs or trees; leaves petiolate, blades deltate or lobate; ligules more than 45 mm long. Species 5 and 6. TYPE: *Tithonia koelzii* McVaugh.

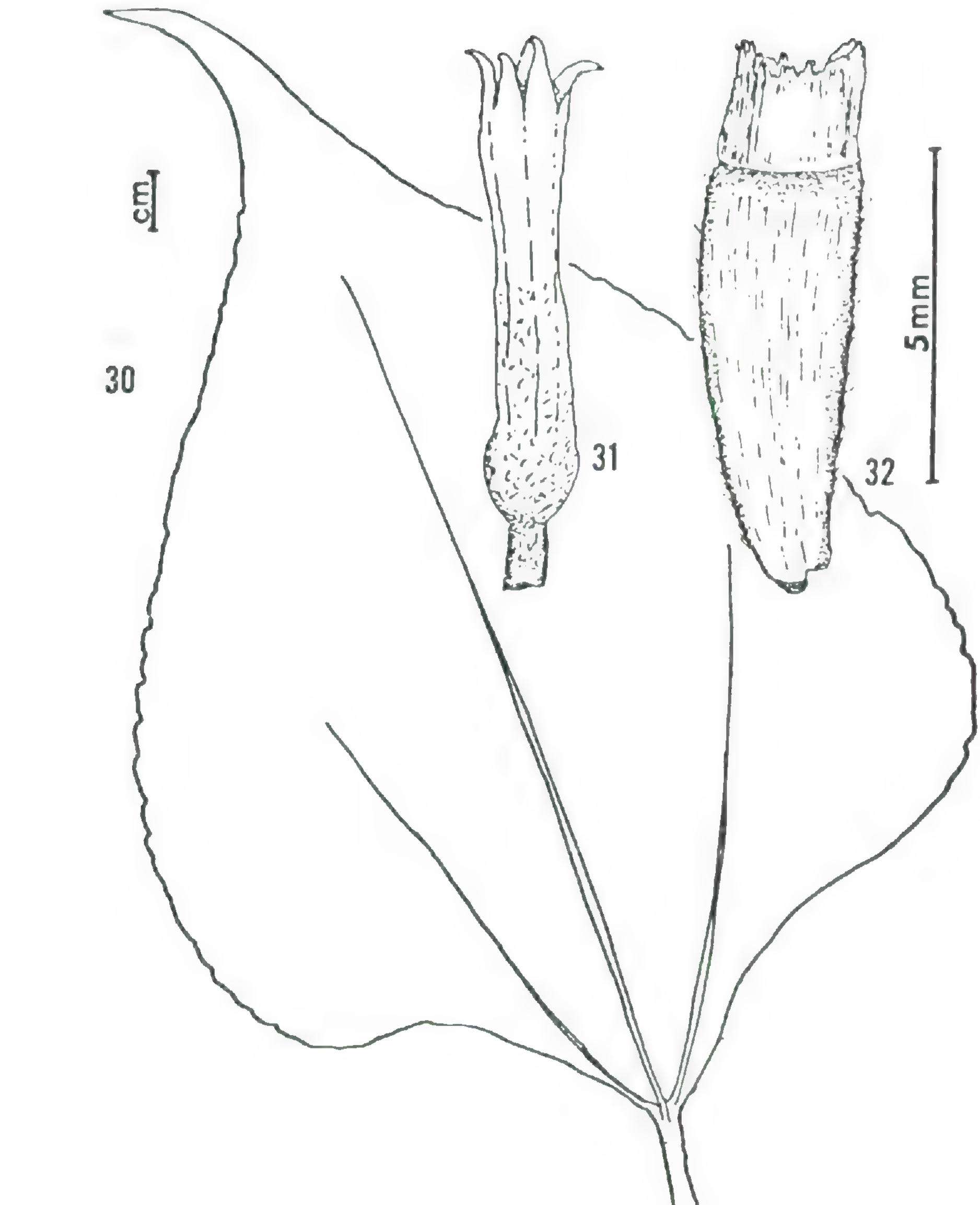
5. **Tithonia koelzii** McVaugh, Contr. Univ. Michigan Herb. **9:** 443. 1972. TYPE: MÉXICO. Jalisco, 12–13 km SE Pihuamo, 500–600m, 15 Dec 1959, *R. McVaugh & W. N. Koelz 1795* (HOLOTYPE, MICH!; ISOTYPES, DUKE!, ENCB!, LL!, NY! US!). Figures 30–32.

Erect, perennial tree, 6–7 m tall. Stems round, brown, 15 cm DBH, sparsely pubescent to glabrous. Leaves alternate with petioles 50–120 mm long with ephemeral auriculae at base; blades deltate, 9.5–19 cm long, 5.8 7 cm wide, at apex acuminate, at base cuneate, on upper and lower surface moderately hispid, at margin crenate. Peduncles 9–12 cm long, 2–4 mm diam, sparsely pubescent to glabrous near head. Heads usually solitary, heterogamous. Receptacle 8 9 mm diam. Phyllaries about 20, three-seriate, graduated, linear to lanceolate; outer bracts 7 mm long, 4 mm wide, at apex acuminate, on abaxial surface glabrous to minutely pubescent; inner bracts 20 mm long, 6 mm wide, at apex rounded, on abaxial surface glabrous to minutely pubescent. Pales striate, 11 mm long, 2 mm wide; apex aristate, 3 mm long, usually with lateral lobes, minutely pubescent. Ray florets 11; ligules yellow, linear, 45 mm long, 17 mm wide, at apex trifid; tube 1.5 mm long, 0.75 mm diam; pappus absent or some scales; achenes one-seriate, dark brown, sterile. Disk florets about 60; corollas yellow; corolla lobes 5, 1.5 mm long, 0.5 mm wide, at apex acute; throat cylindrical with expanded minutely pubescent base, with cylindrical portion 4.5–5 mm long, 1–1.5 mm diam, with expanded portion 1.5 mm long, 1.5 mm diam; tube minutely pubescent, 1 mm long, 0.5 mm diam; anthers tan, 5 mm long; styles 11.5 mm long; stigmas pappillate, 3.5 mm long; pappus ring of fused squamellae; achenes fertile, black, brown, pubescent, particularly on the edges, quadrangular, 6.5 7 mm long, 3 mm diam, at base smooth without eliasome. Chromosome number $n = 17$ (counted as $2n = 34 + 4–5$ B).

PRINCIPAL FLOWERING TIME: October to November.

DISTRIBUTION: Known only from the type locality in Jalisco, México (Fig. 33).

Tithonia koelzii is a small tree, and the peduncle is the least flared of all taxa of the genus. *Tithonia koelzii* is one of two taxa, the other *T. diversifolia,* with auriculae at the base of the petiole which are ephemeral. These laminar auriculae are produced on older mature



Figures **30–32.** Leaf (**30;** *La Duke et al.* 477, OS), disk corolla (**32**), and disk achene (**31**) of *Tithonia koelzii.* Figs. 31 and 32; *McVaugh and Koelz 1504* (MICH); same scale.

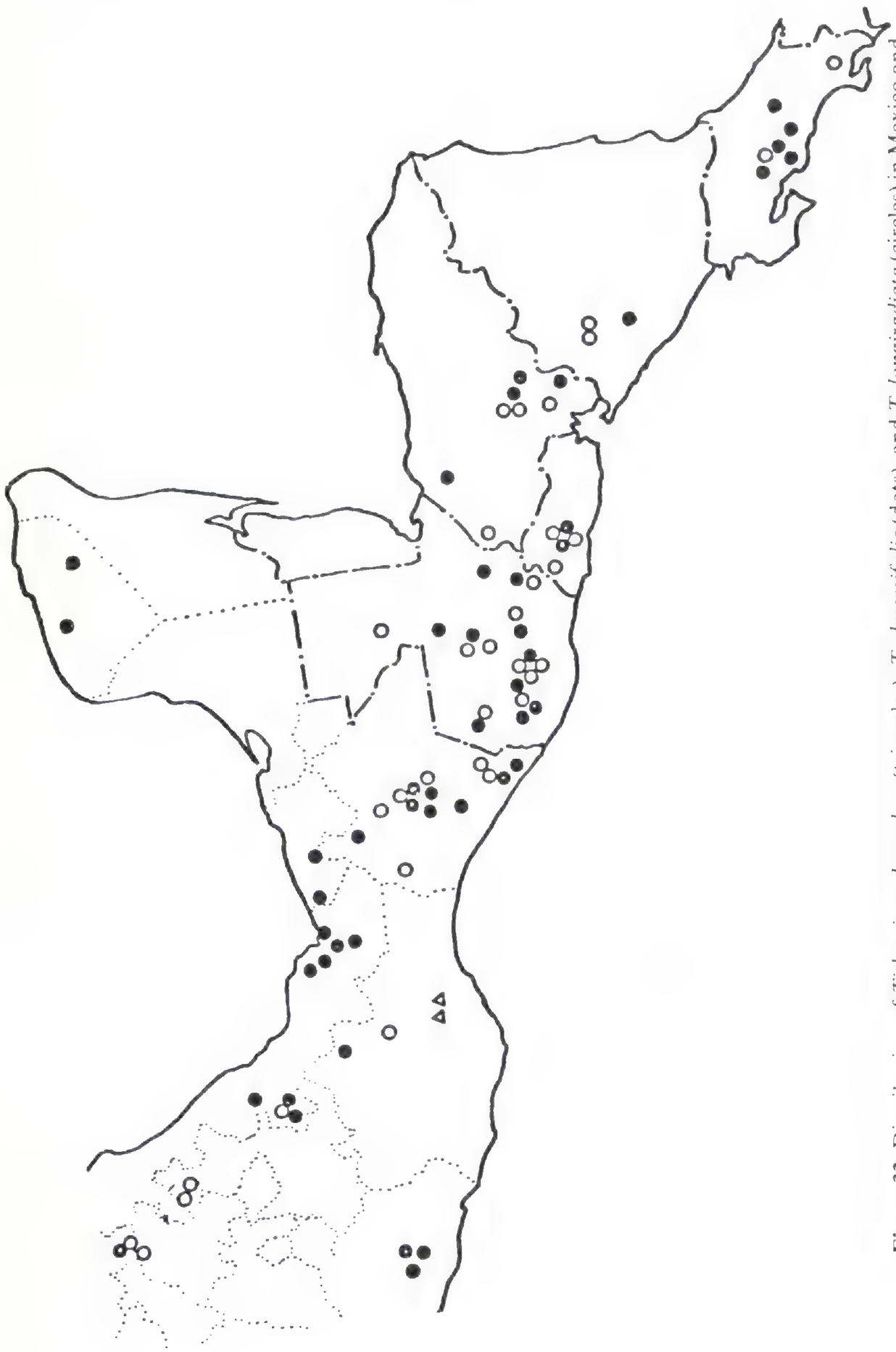


Figure 33. Distribution of *Tithonia peduncularata* (triangles), *T. diversifolia* (dots), and *T. longiradiata* (circles) in Mexico and Central America.

leaves, and when the plants are stressed, they dry and brown, and may be difficult to detect. Chromosomally, *T. koelzii* is diploid at $n = 17$, but has an additional complement of 5 to 6 B-chromosomes.

REPRESENTATIVE SPECIMENS. MÉXICO. **Jalisco:** 12–13 km SW of Pihuamo, 500 600m, *McVaugh & Koelz 1504* (DUKE, ENCB, MICH, NY), *McVaugh 24496* (DUKE, ENCB, LL, MICH), *La Duke et al. 477** (OS).

6. **Tithonia diversifolia** (Hemsl.) A. Gray, Proc. Amer. Acad. Arts **19:** 5. 1883 Figures 34–36.

Mirasolia diversifolia Hemsl. in Godman & Salvin, Biol. Centr. Amer. Bot. **2:** 168. *t. 47.* 1881. TYPE: MÉXICO, Veracruz, Valley of Orizaba, 12 May 1866, *E. Bourgeau 2319* (LECTOTYPE, K!, [photo, OS!]; ISOLECTOTYPES, BR!, FI!, GH!, S!, US!).

Urbanisol tagetifolius var. *diversifolius* f. *grandiflorus* O. Kuntze, Rev. Gen. Pl. **1:** 370. 1891. TYPE: Singapore, date unknown, probably collected by *O. Kuntze s.n.* (HOLOTYPE, not located). This taxon is placed here based on specimens annotated by Kuntze.

Urbanisol tagetifolius var. *flavus* O. Kuntze, Rev. Gen. Pl. **1:** 1875. TYPE: Singapore, Oct 1875, *O. Kuntze 6074* (HOLOTYPE, NY!; ISOTYPE, K!).

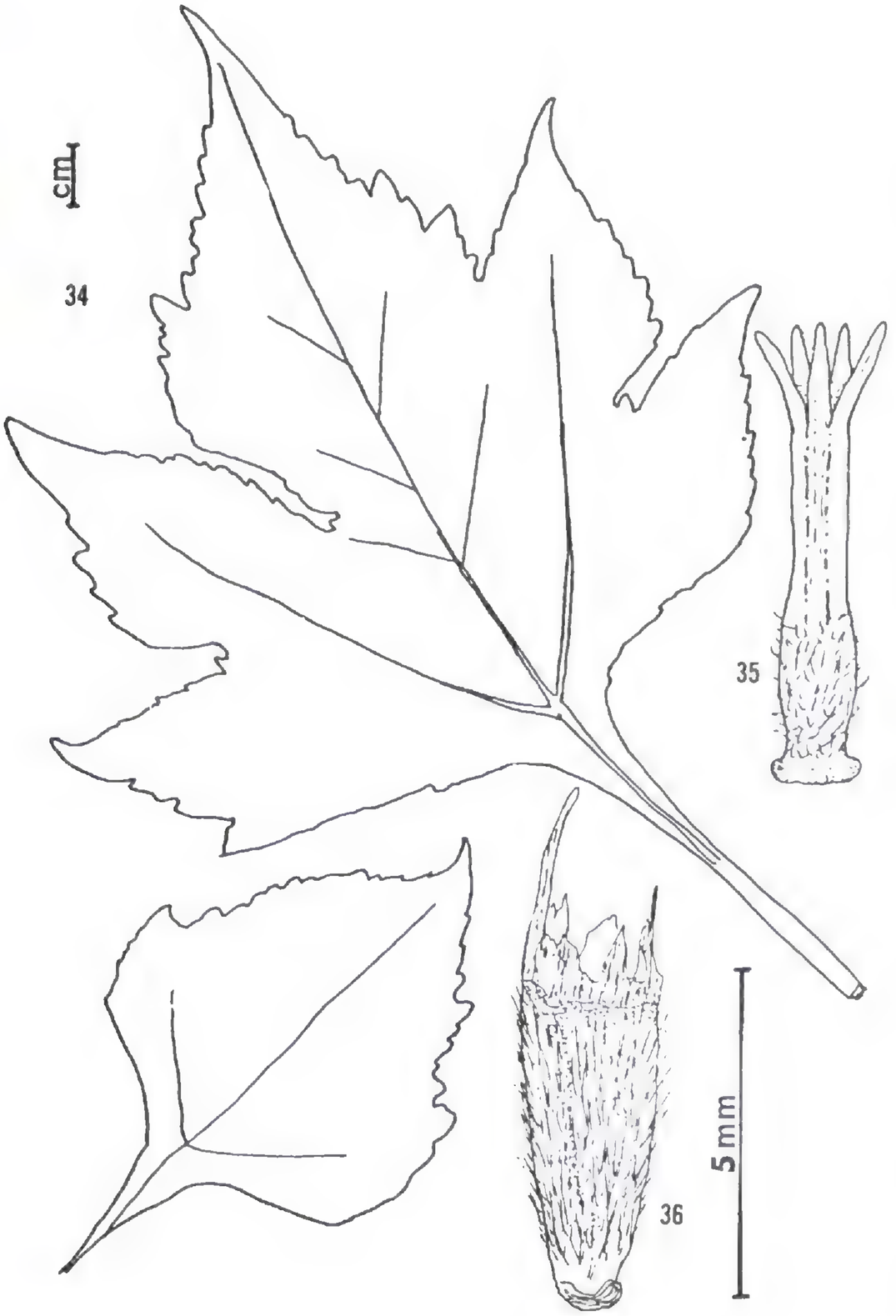
Urbanisol tagetifolius var. *diversifolius* (Hemsl.) O. Kuntze, Rev. Gen. Pl. **1:** 371. 1875.

Tithonia trilobata Sch.-Bip. in Klatt, Bull. Soc. Bot. Belg. **31:** 203. 1891. *Nom. nud. pro. syn.* Based on the following cited specimen: Mirador, Nov 1841, *F. M. Liebmann 603* (C!, P!, [photo, OS!]).

Helianthus quinquelobus Sesse & Mocino, Fl. Mex. ed. 2. 193. 1894. TYPE: MÉXICO, Veracruz, Orizaba, *M. Sesse & J. M. Mocino s.n.* [Madrid herb. 2936] (LECTOTYPE here chosen; M!).

Tithonia diversifolia var. *glabriscula* S. F. Blake, Contr. U.S. Nat. Herb. **20:** 435. 1921. TYPE: MÉXICO, Oaxaca, N of Tuxtepec, 90 m, 9 Apr 1894, *E. W. Nelson 346* (HOLOTYPE, US!).

Erect, perennial, herbaceous, 2.5–5 m tall. Stems round, usually brown to green, glabrous to villous. Leaves alternate, sessile or with petioles to 6 cm long; blades deltate to 3–5 lobed, 7 33 cm long, 7 22 cm wide, at apex acuminate, at base attenuate, ephemeral auricle at base of petiole, on upper surface glabrous to hispid-pilose, on lower surface glabrous to villous, at margin serrate. Peduncles 7–24 cm long, 4–13 mm diam, sparsely tuberculate-hispid. Heads usually solitary, heterogamous. Receptacle 7 13 mm diam. Phyllaries 16–28, (three-) four-seriate, graduated, oblong to ovate, outer bracts 6–10 mm long, 4–7 mm wide, at apex rounded to acute, occasionally scarious, on abaxial surface usually glabrous; inner bracts 10–20 mm long, 3 10 mm wide, at apex rounded to acute, on abax-



Figures **34**–**36**. Leaf outlines (**34**, *La Duke et al. 569a*, OS), disk corolla (**35**), and disk achene (**36**) of *Tithonia diversifolia*. Figures 35 and 36, *Feddema 2889*, TEX; same scale.

ial surface glabrous. Pales striate, 10–13 mm long, 2–3 mm wide; apex aristate, 1.5–2.5 mm long, usually with lateral lobes, minutely pubescent occasionally toward apex or on fold. Ray florets 7–14; ligules yellow, linear, 48–69 mm long, 9–16 mm wide, at apex trifid; tube 2–2.5 mm long, 1–1.5 mm diam; pappus absent or paleaceous ring; achenes one-seriate, white to yellow, sterile. Disk florets 80–120; corollas yellow; corolla lobes 5, 1–1.5 mm long, 0.5 mm wide, at apex acute; throat cylindrical with expanded minutely pubescent base, with cylindrical portion 3–4 mm long, and 0.75 mm diam, with expanded portion 1.5–3 mm long, 1–1.5 mm wide; tube partially minutely pubescent, 0.75–1 mm long, 0.75 mm diam; anthers black, 4–5 mm long; styles 9–12 mm long; stigmas pappillate, 2–3 mm long; pappus of fused squamellae, 2 subequal awns; achenes fertile, black or mottled, puberulent, quadrangular, 5–6 mm long, 1.5–2 mm diam at base smooth without eliasome. Chromosome number, $n = 17$.

PRINCIPAL FLOWERING TIME: September to January.
DISTRIBUTION: Tropical México and Central America (Fig. 33).

Tithonia diversifolia is the most widespread of the taxa of *Tithonia*. It has been successfully cultivated in Africa, Australia, Asia, and North America where it has escaped and is now locally abundant. It is a weedy herbaceous perennial, most closely related to *T. koelzii* (see *T. koelzii* for discussion), but it most often is confused with *T. rotundifolia* because of its similar 3–5 lobed leaves and hearty habit.

REPRESENTATIVE SPECIMENS. AUSTRALIA. **N. Queensland:** near Tolga, *McKee 9394* (K). **New South Wales:** Coffs Harbor, *Covney 9426* (RSA). BERMUDA. Harrington House Garden, *Brown et al. 2267* (NY). BRITISH NORTH BORNEO. Sandakan, *Wood 1164* (UC). BURMA. Rangoon, *Dickason 5234* (GH). CAMEROON. 10 km S of Ngaoundere, *Amshoff 256* (K). CANARY IS. **Tenerife:** Puerto de Guimar, *Hansen 1036* (C). COSTA RICA. **Heredia:** along rd to Concepción, ca 2 km N of San Isidro, *King 6793* (F). **San José:** Tabarcia, *Jimenez 655* (CR, F, NY). CUBA. Pinar del Río, *Alain & Killip 2026* (NY, US). DOMINICAN REPUBLIC. Santiago, *Jiménez 975* (US). EL SALVADOR. **Ahuachapán:** Ataco, *Standley & Padilla 2646* (F). GHANA. no locality, *Akpabla 1962* (K). GUATEMALA. Antigua, *Holiway 65* (GH). **Alta Verapaz:** .5 mi NE of San Pedro Carchá on rd to Sebol, *Jansen & Harriman 526* (OS). **Chiquimula:** 2.6 mi SE Quezaltepeque, *La Duke et al. 531* (OS). **Huehuetenango:** 24 mi NW Huehuetenango on rte ca-1, *La Duke et al. 535** (OS). **Quezaltenango:** below Santa María de Jesús, *Jansen & Harriman 521* (OS). HONDURAS. **Choluteca:** between El Chinchayote and Comali, *Molina 24581* (MO, NY, US). **Morazán:** ca 18 mi S of Tegucigalpa on rte 1, *Stuessy & Gardner*

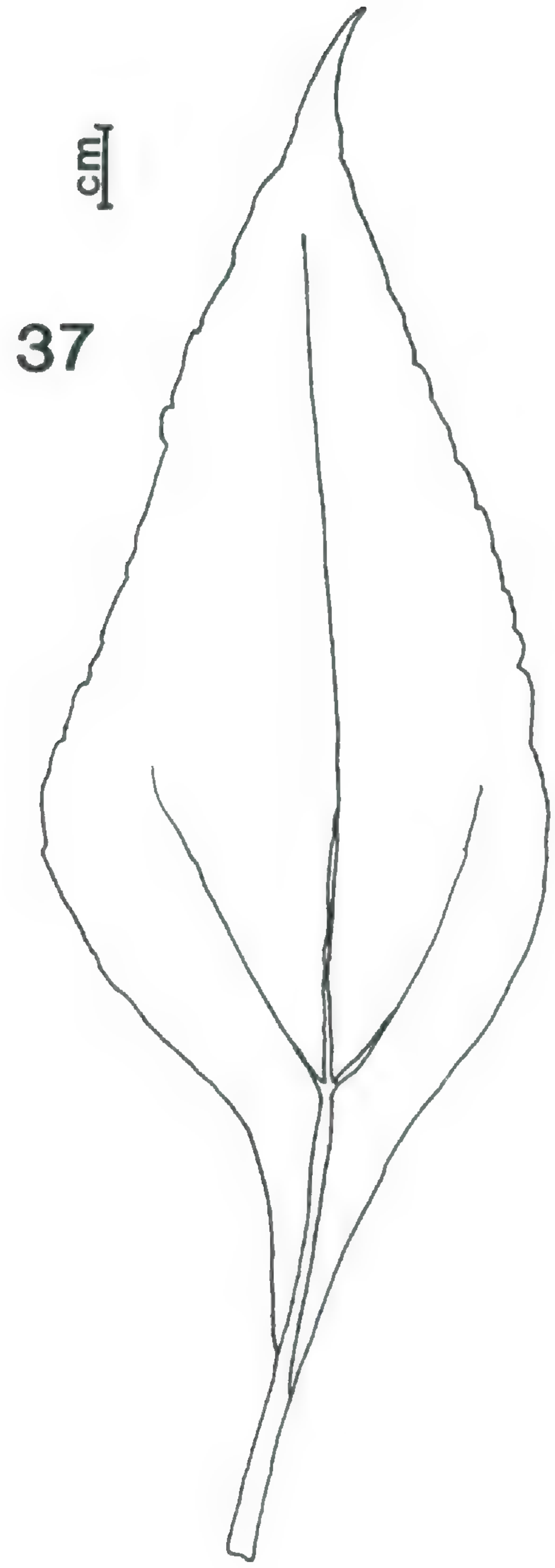
4424 (OS). INDIA. **Assam:** Bamanigaon, *Chand 2496* (UC). INDOCHINA. Gourane, *Poilane 1442* (UC). IVORY COAST. Gagnoa, *Sundell 289* (NA). KENYA. Mutuati-Nyambeni Highlands, *Hanid & Kiniaruh 1003* (MO). MALAWI. **Dedza:** Dedza, *Brummit 10415* (K). MALAYSIA. **Malacca:** no locality, *Vesterdal 397* (C). MÉXICO. **Chiapas:** about 23 mi W of San Cristóbal de las Casas, *Cronquist 9674* (GH, MICH, MO, NY, TEX, US); ca 20 mi E of Tuxtla Guitérrez on rte 190, *Stuessy & Gardner 4299* (OS); 6.5 mi W of Apaz on rte 190, *La Duke et al. 523** (OS). **Guerrero:** Cruz de Ocote, ca 25km SWS of Camolta, *Feddema 2889*, (DS, DUKE, ENCB, MO, MICH, NY, TEX); **Oaxaca:** Chiltepec, *Calderon 446* (GH, LL, MEXU, UC, US); .2 mi N of Tuxtepec, *La Duke & Jansen 403** (OS). **Tabasco:** 4.7 mi E of Cárdenas on rte 180, *La Duke et al. 564** (OS). **Veracruz:** Btwn San Andres Tuxtla and Catemaco, *Cronquist & Sousa 10360* (DS, DUKE, ENCB, GH, MEXU, MICH, NY, TEX, US); 1.1 mi E of rd to Cuautlapan on rte 150, *La Duke et al. 568a* (OS). **Yucatán:** Mérida, *Sousa 5* (NA). NIGERIA. **Calabar:** Calabar, *Daramola 55325* (K). PANAMA. **Cocle:** 1.9 mi S of El Valle, *Stuessy & Gardner 4529* (OS). PHILIPPINES. **Mindoro Is:** Puerto Galera, *Velasquez 25* (GH). PUERTO RICO. along rd near Florida, *Wagner 791* (A). S. RHODESIA. **Umtali:** no locality, *Chase 4632* (K, MO). SEYCHELLE IS. Victoria, *Jeffrey 750* (K). SRI LANKA. Peradeniya, *Comandor 318* (MO). SUMATRA. Vicinity of Rantau, *Toroes 1941* (DS, VC). TAHITI. rd. between Papeete & Papeari, *Setchell & Parks 227* (GH, UC). TANZANIA. roadside near Chemka, *Baagoo et al. 159*. (C). THAILAND. Bangkok, *Sorensen et al. 1986* (C, K). TRINIDAD. Blanchisseuse Rd, *Ross 1020* (A). UNITED STATES. **Florida:** Hernando City, Chinsegut Hill, *Colley 6333* (FSU); ca 3 mi W Brooksville, Fla 50, *Beckner 796* (FSU, GH). **Hawaii:** Lawai Valley, *Herbst 2270* (GH); E Manoa rd, Honolulu, *Bush 107* (NA). WEST INDIES. HAITI: Bodarie to Thiote, *Holdridge 2036* (MICH, NY, US). ZAIRE. environs of Lubumbashi, *Quarre 5400* (MO).

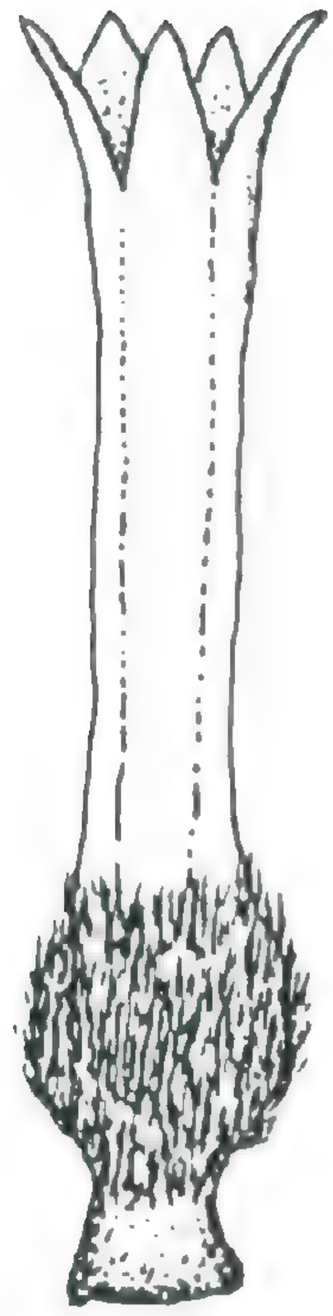
3. Series *Fruticosae* La Duke. Rhodora **84:**140–141. 1982.

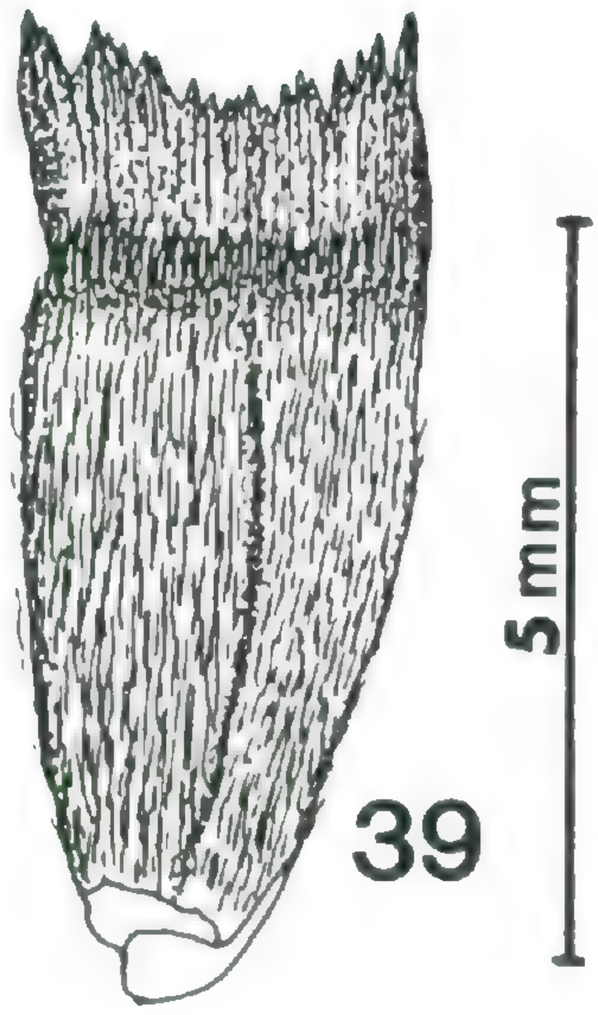
Plants perennial shrubs; leaves lanceolate, sessile or petiolate; phyllaries in 3 or 4 series; achenes quadrangular. Species 7 and 8. TYPE: *Tithonia fruticosa* W. M. Canby & J. N. Rose in J. N. Rose.

7. **Tithonia fruticosa** W. M. Canby & J. N. Rose in J. N. Rose, Contr. U.S. Nat. Herb. **1:** 104. *pl. 5*. 1891. TYPE: MÉXICO, Sonora, among bushes near a watercourse, Alamos, Mar – Apr 1890, *E. Palmer 303* (LECTOTYPE here chosen, US!; ISOLECTOTYPES, A!, GH!, K [photo, OS!], NY!, US!). Figures 37–39.

Erect, perennial, shrub, 2–3 m tall. Stems round, gray to brown, minutely soft-woolly. Leaves alternate, sessile or with petioles to 30 mm long; blades lanceolate-deltate, 9 23 cm long, 4.5 9 cm wide, at apex long acuminate, at base attenuate, on upper and lower surfaces soft-woolly, at margin serrate to crenate. Peduncles







Figures **37–39.** Leaf (**37**), disk corolla (**38**), and disk achene (**39**) of *Tithonia fruticosa* (*Weber & Bye 8352*, OS). Figures 38–39, same scale.

5.4–12 cm long, 4–7 mm diam, densely woolly. Heads usually solitary, heterogamous. Receptacle 10–15 mm diam. Phyllaries about 24, four-seriate, graduated, ovate; outer bracts 9–14 mm long; 5–11.5 mm wide, at apex rounded, on abaxial surface minutely soft-pubescent; inner bracts 14–21 mm long, 5–8.5 mm wide, at apex rounded, on abaxial surface minute soft-pubescent. Pales striate, 11.5–15 mm long, 1.5–3 mm wide; apex acute to aristate, 3–5 mm long, usually with secondary lobes, usually minutely hispid apically. Ray florets 14–19; ligules yellow, linear, 25–41 mm long, 5.5–11 mm wide, at apex trifid; tube 3 mm long, 0.75–1.5 mm diam; pappus absent; achenes one-seriate, yellow to brown, sterile. Disk florets 100–120; corollas yellow above, dark below; corolla lobes 5, 1–1.25 mm long, 0.5 mm wide, at apex acute; throat cylindrical with expanded minutely pubescent base, with cylindrical portion 4–5 mm long, and 0.75–1 mm diam, with expanded portion 1.5–2 mm long, and 1–1.75 mm diam; tube minutely pubescent, 1–2 mm long, 0.75–1 mm diam; anthers tan, 4.5–5 mm long; styles 9–12 mm long; stigmas papillate, 2–4 mm long; pappus of fused squamellae; achenes fertile, gray to brown to black, pubescent, quadrangular or subquadrangular, 4.5–6 mm long, 2–2.5 mm diam, smooth at base without eliasome. Chromosome number, $n = 17$.

PRINCIPAL FLOWERING TIME: March-April.

DISTRIBUTION: Canyons and slopes in the Mexican states of Chihuahua, Durango, Sinaloa, and Sonora, usually near water (Fig. 22).

Tithonia fruticosa is a weak perennial shrub which branches from the base. It is easily recognized by its lanceolate, acuminate-tipped leaves which, like the branches, are densely soft-pubescent, and by its broadly ovate phyllaries. *Tithonia fruticosa* is restricted in distribution to northwestern Mexico, where it grows in mesic habitats.

REPRESENTATIVE SPECIMENS. MÉXICO. **Chihuahua:** near Batopilas, *Goldman 232* (US); Sierra Orejon Río Mayo upper Sonora, *Gentry 1219* (F, NA); Barranca del Cobre, *Knobloch 7031* (US); Barranca del Cobre, S wall of Guacaybo arroyo, *Hewitt 21* (GH); downslope from Guageybo, *Pennington 57* (TEX); La Bufa, SE of Creel, *Knobloch 512* (SMU); Santa Rose, *Pennington 337* (TEX); La Bufa, *Weber & Bye 8352** (OS). **Durango:** San Ramon, *Palmer 68* (F, MO, NA, NY, UC, US); Tayoltita, *White 5002* (MICH). **Sinaloa:** Sierra de Los Álamos, *Palmer 303* (A, GH, NY, US); Puerta a Tamiapa, *Gentry 5845* (ARIZ, GH, MICH, MO, NA, NY). **Sonora:** Huchuerachi, *Hartman 301* (GH, NY); vicinity of Álamos, *Rose 13085* (C, F, GH, MO, NY, US); canyon

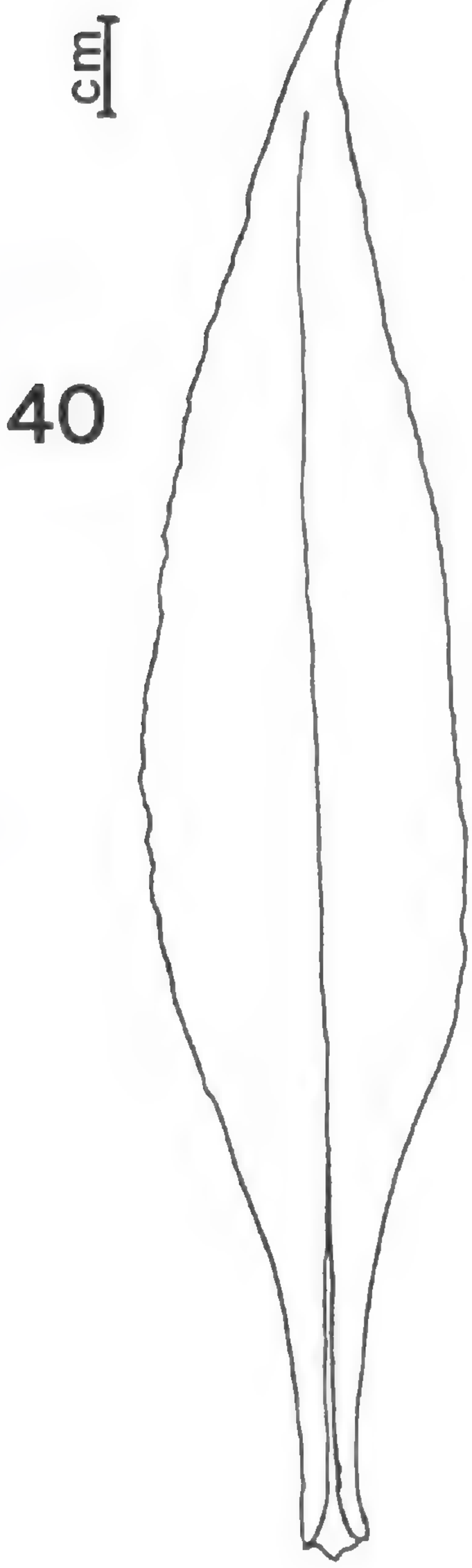
Saucito, *Gentry 703M* (MICH); canyon Narcissus, Río Mayo, *Gentry 1182* (F, MO); Dist. of Álamos, spring 1935, *Gentry s.n.* (NA); Curohui, Río Mayo, *Gentry 3645* (MO); 4 mi S of Mazocahui, *Turner 59 70* (ARIZ, OS, US); 1 mi S of Santa Ana, *McLaughlin 524* (ARIZ).

8. **Tithonia pedunculata** A. Cronquist, Mem. New York Bot. Gard. **12:** 286. *Fig. 1.* 1965. TYPE: MEXICO, Oaxaca, 42 mi NW of Tehuantepec, ca. 2300 ft, *A. Cronquist 9684* (HOLOTYPE, NY!; ISOTYPES, F, GH!, MICH!, MO!, TEX!, US!).
Figures 40–42.

Erect, perennial shrub, 1–3.2 m tall. Stems round, brown, usually glabrous. Leaves alternate, with petioles to 3 mm long or sessile; blades linear-lanceolate, 7.5–23.5 cm long, 1.5 5.0 cm wide, at apex acuminate, at base attenuate, on upper surface hispid, on lower surface hispid to villous, at the margin entire to weakly crenate. Peduncles 11 27 cm long, 2 9 mm diam, sparsely to moderately pubescent near the head. Heads usually solitary, heterogamous. Receptacle 10 12 mm diam. Phyllaries 22 32, three-seriate, graduated, linear; outer bracts 6–11 mm long, 2–4 mm wide, at apex acute, on abaxial surface minutely pubescent; inner bracts 14–18 mm long, 3.5 6 mm wide, at apex acute or rounded, on abaxial surface minutely pubescent toward apex. Pales striate, 11–14 mm long, 2.5–3 mm wide; apex acuminate, 5–6.5 mm long, usually with secondary lobes, minutely pubescent. Ray florets 13–15; ligules yellow, oblong, 21–31 mm long, 6–8.5 mm wide, at apex trifid; tube 1–1.5 mm long, 0.5–1 mm diam; pappus absent or some small scales; achenes one-seriate, triangular, white-tan, sterile. Disk florets 90–100; corollas yellow; corolla lobes 5, 0.75 1.5 mm long, 0.5 mm wide, at apex acute; throat cylindrical with expanded minutely pubescent base, cylindrical portion 2.5–3.5 mm long, 1–1.5 mm diam, with expanded portion 1.5–3 mm long, 1.5–2 mm diam; tube minutely pubescent, 0.5–1 mm long, 0.75 1 mm diam; anthers black, 3–5 mm long; styles 6 7.5 mm long; stigmas pappillate, 2–3 mm long; pappus a ring of fused squamellae with two awns; achenes fertile, quadrangular, black, 4.5 5 mm long, 1.75 2.5 mm diam, with eliasome at base. Chromosome number, $n = 17$.

PRINCIPAL FLOWERING TIME: September-October.

DISTRIBUTION: Restricted to central Oaxaca, México in xeric habitats (Fig. 33).



Figures **40–42.** Leaf (**40**; *La Duke et al. 408;* OS), disk corolla (**41**; *La Duke et al. 408,* OS), and disk achene (**42**; *La Duke et al. 410,* OS) of *Tithonia pedunculata.* Figures 41 and 42 same scale.

Tithonia pedunculata is an attractive shrub known from Oaxaca, México. It is most closely related to *T. fruticosa* of Chihuahua, Durango, Sinaloa, and Sonora. *Tithonia pedunculata* has narrower phyllaries, branches above the base, sparse to moderate pubescence on leaves, and is limited in distribution. *Tithonia pedunculata* is also the only member of this section with pappus and an eliasome. Eliasomes have been shown to be important in dispersal of achenes of Compositae by ants (Nesom, 1981), but these taxa usually have epappose achenes. The dispersal mechanism of this taxon warrants further investigation.

REPRESENTATIVE SPECIMENS. MEXICO. **Oaxaca**: Isthmus of Tehuantepec, *Paray 222* (ENCB); along rte 190 ca 42 mi W of Tehuantepec, *King 2472* (MICH, TEX); along rte 190 ca 61 mi W of Tehuantepec, *King 2474* (DS, MICH, TEX); 2 mi S of El Camaron, *Breedlove 7168* (DS, MICH, MO, NY); hwy 190, 69 mi NW of Tehuantepec, *Lathrop 6723* (DS, RSA); ca 98 km NW of Tehuantepec, *Cronquist & Fay 10859* (ENCB, NY); 8 mi W of Las Minas, *Wunderlin et al. 841* (MO); .9 mi NW Las Majadas on hwy 190, *La Duke & Jansen 408** (OS); 41.3 mi NW Tehuantepec on hwy 190, *La Duke & Jansen 409** (OS); 3 mi NW of Las Minas on rte 190, *La Duke & Jansen 410* (OS); ca 38 mi SE of Totolapan on rte 190, *Stuessy & Gardner 4276* (OS); 4.3 mi N of Las Animas on rte 190, *La Duke et al. 508* (OS); 6 mi N of bridge over Río Cameron, hwy 190, *Jansen & Harriman 500* (OS).

II. *Tithonia* section *Mirasolia* (Sch.-Bip. in Seemann) La Duke. Rhodora **84**:141. 1982.

Tithonia Gmelin subgen. *Mirasolia* Sch.-Bip. in Seemann Bot. Voyage Herald. 305. 1856.

Perennial shrubs; leaves linear to ovate, usually sessile to short-petiolate, margins serrate to crenate; phyllaries 3 4(5)-seriate; disk achenes rounded-quadrangular, epappose, glabrous, with eliasome at base. Species 9–11. TYPE SPECIES: *Tithonia calva* Sch.-Bip. in Seemann.

9. **Tithonia calva** Sch.-Bip. in Seemann, Botany Voyage Herald. 305. 1856.

Erect, perennial, shrub, 0.5–3 m tall. Stems round, tan, brown, to 2 cm diam, sparsely pubescent to villous with hairs 15 mm long. Leaves alternate, sessile; blades linear-lanceolate, ovate-lanceolate, to rounded triangular, 5.7–32.5 cm long, 1.1–17 cm wide, at apex acuminate, at base attenuate, auriculate, on upper and lower surface

sparsely to densely pubescent, at margin serrate to crenate. Peduncles 5.5–15.5 cm long, 2–13 mm diam, moderately hispid to woolly near head. Heads usually solitary or in small clusters, heterogamous. Receptacle 6 14 mm diam. Phyllaries 16 29, three-(four)-seriate, graduated, linear to lanceolate; outer bracts 5.5–14 mm long, 1.5–3.5 mm wide, at apex acute to acuminate, on abaxial surface hispid-pilose, occasionally indurate below; inner bracts 6.5 mm long, 1.5–5 mm wide, at apex rounded to acute, on abaxial surface hispid-pilose. Pales striate, 5–10 mm long, 1.5–3.5 mm wide; apex aristate to acute, 0.5–3 mm long, with or without lateral lobes, minutely hispid towards apex. Ray florets (8–) 11–18; ligules yellow, linear to oval-oblong, 17 40 mm long, 4–12 mm wide, at apex trifid; tube 1–2 mm long, 0.5 1.5 mm diam; pappus absent; achenes one-seriate, white to yellow, sterile. Disk florets 60–140; corollas yellow; corolla lobes 5, 0.5–1 mm long, 0.5 mm wide, at the apex acute; throat cylindrical with expanded minutely pubescent base, with cylindrical portion 1.5–4 mm long, 0.75–1.25 mm diam, with expanded portion 1–1.5 mm long, 1–2 mm diam; tube minutely pubescent, 0.5 11 mm long, 0.75 1.25 mm diam; anthers tan-brown or black, 3.5 mm long; styles 4.5–6.5 mm long; stigmas pappillate, 1.2–2.5 mm long; pappus absent; achenes fertile, black or mottled, rounded-quadrangular, 3–5 mm long, 1 2 mm diam, with an eliasome at base. Chromosome number, $n = 17$.

9a. **Tithonia calva** Sch.-Bip. in Seemann, var. **calva.** Figs. 43 45.

Tithonia calva Sch.-Bip. in Seemann, Botany Voyage Herald. 305. 1856. TYPE: MÉXICO, Sierra Madre, *B. C. Seemann 2045* (HOLOTYPE, P [photo, OS!]; ISOTYPES, K! [photo, GH!]).

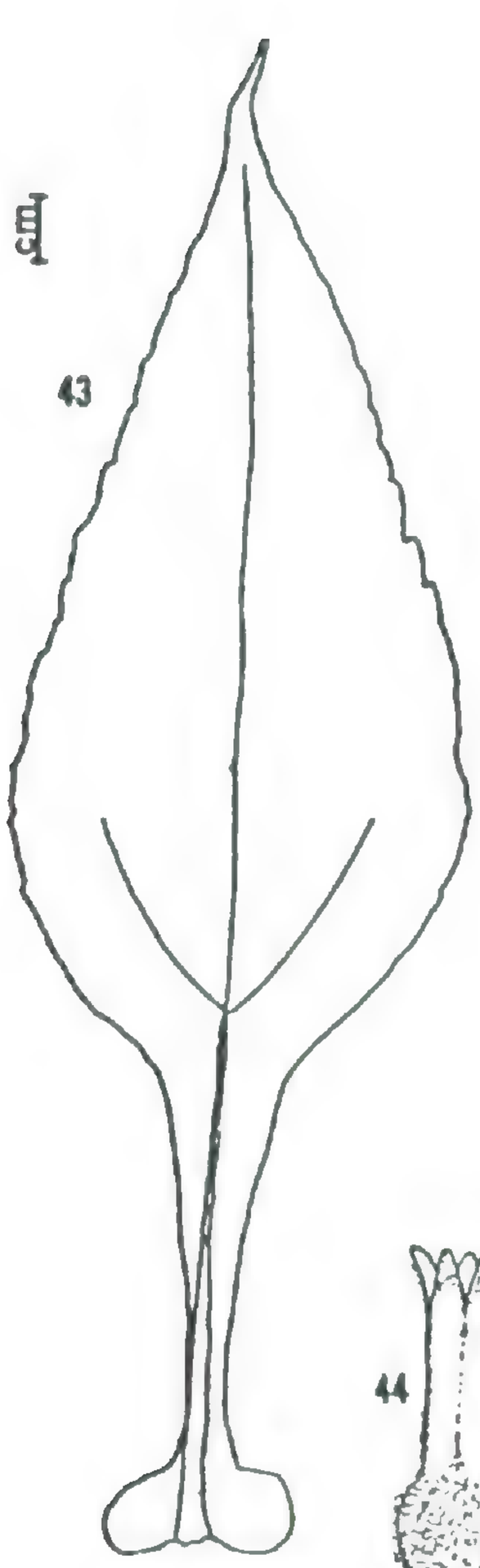
Mirasolia calva (Sch.-Bip. in Seemann) Benth. & Hook. ex Hemsl. in Godman & Salvin, Biol. Centr. Amer. Bot. **2:** 168. 1881.

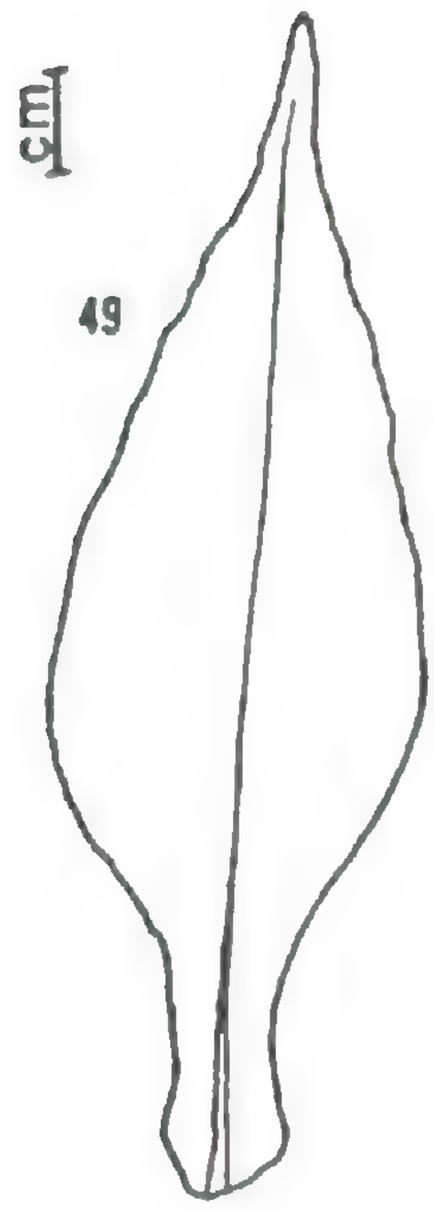
Gymnolomia calva (Sch.-Bip. in Seemann) A. Gray, Proc. Amer. Acad. Arts **19:** 5. 1883.

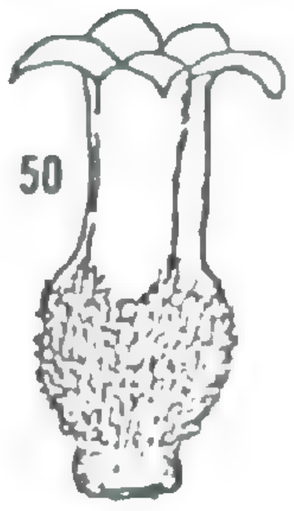
Stems usually with long (to 15 mm) hairs. Leaves ovate-lanceolate to rounded-triangular, 9–32.5 cm long, 4–17 cm wide. Receptacle 10–14 mm diam. Disk florets 120–140.

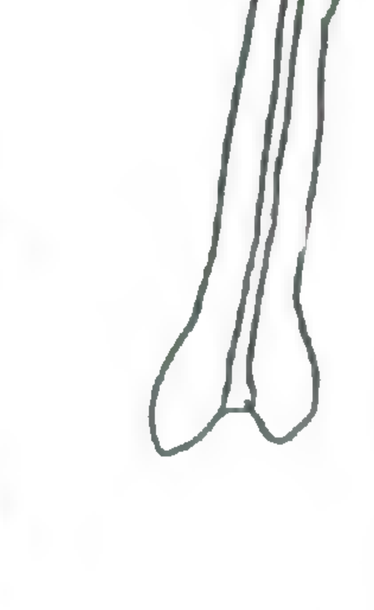
PRINCIPAL FLOWERING TIME: August-November.

DISTRIBUTION: In the Mexican states of Chihuahua, Durango, Nayarit, Sinaloa. Fig. 22.









Figures **43–51.** Leaf, disk corolla, and disk achene of the three varieties of *Tithonia calva.* Leaf (**43**; *La Duke et al. 387,* OS), disk corolla (**44**; *Cronquist 10550,* MICH), and disk achene (**45**; *Cronquist 10550,* MICH) of *Tithonia calva* var. *calva.* Leaf (**46**; *La Duke et al. 430,* OS) disk corolla (**47**; *Gentry 5144,* ARIZ), and disk achene (**48**; *La Duke et al. 430,* OS) of *Tithonia calva* var. *auriculata.* Leaf (**49**; *Lamb 539,* DS), disk corolla (**50**; *McVaugh 23555,* US), and disk achene (**51**; *McVaugh 23555,* US) of *Tithonia calva* var. *lancifolia.* Figures 44 and 45 same scale; figures 47, 48, 50, 51 same scale.

Tithonia calva var. *calva* is readily distinguished by its epappose achenes and ovate to broadly lanceolate sessile auriculate-based leaves. The plants have been obtained primarily on Mexican Hwy 40 between Durango and Mazatlán in the high mountains, however, populations as far north as Chihuahua indicate it may be present throughout the western mountains, but in areas not readily accessible.

The most closely related species to *Tithonia calva* var. *calva* is *T. longiradiata*. These two taxa differ in a number of characteristics respectively, such as: 1) auriculate leaf base vs. attenuate, 2) linear to oblong phyllaries vs. spathulate phyllaries, and 3) distribution Northwestern México vs. Southeastern México, (Figure 22 vs 33).

REPRESENTATIVE SPECIMENS. MÉXICO. **Chihuahua:** Guasaremos Río Mayo, *Gentry 2900* (F, GH, K, MO, S, UC). **Durango:** 27.4 mi SW of Buenos Aires, *Ownbey & Ownbey 1884* (MICH); without locality, 15 Aug 1897, *Rose 2293* (GH); El Salto 3 km E of Sinaloa state line, *Detling 8598* (US); ca 3 km E of Sinaloa-Durango boundary on hwy from Villa Union, *Feddema 1822* (DUKE, ENCB, MICH); 1 mi above Revolcadero on hwy 40, *Weber & Charette 11799* (MICH); 1 mi W Revolcadero, *Flyr 300* (TEX); 2 mi NE of Durango-Sinaloa border along rte 40, *Torres 1775* (MICH); 1175 km post, hwy 40, *Walker 9* (NY); 1180 km post, hwy 40, May 1970, *Henze & Henze s.n.* (TEX); 87 mi E Mazatlán, hwy 40, *Reveal & Atwood 3619* (US); in Revolcadero on hwy 40, NW end of town, *La Duke et al. 385** (OS); 5.7 mi SE of Revolcadero on hwy 40, *La Duke 386** (OS). **Sinaloa:** 49 mi E of Villa Union, *Wiggins 13182* (DS); 2 mi NE of Revolcadero, *Waterfall 12728* (SMU); Palmito & vicinity, *Gentry & Arguelles 18183* (US); 22.1 mi E of Río Concordia at Concordia, rte 40, *Breedlove 1645* (DS, DUKE, MICH); Villa Union, *Van Den Bosch 64–2–1C* (UC); 15 km above Santa Lucia, *McVaugh 23586* (DS, DUKE, ENCB, LL, MICH, NY); 12 miles SW of El Palmito, *Cronquist 10550* (DS, ENCB, GH, MEXU, MICH, NY, US); La Lobera, *Hernandez 442* (LL); ca 27 mi E of hwy 15 on hwy 40, *Spetzman 1190* (NA); 13 mi SW el Palmito, *Webster & Brecken 15535* (GH, LL, MICH); Panuco, *Smith 183* (ARIZ); 6.8 mi NE of Santa Lucia on rte 40, *Keil & Canne 8845* (OS); along hwy 40 ca 8 mi W of Las Palmitas, *Norris et al. 20286* (DS); 1 mi SW of Santa Lucia along rte 40, *Roberts & Keil 10189* (OS, POM); Palmito, *Pinkava et al. P12913* (ENCB, OS); 2 mi before Potrerillos on rd from Mazatlán to Durango, *Kimmach & Sanchez-Mejorada 1646* (MEXU); Santa Rita on hwy 40, *La Duke 387** (OS); hwy 40 ca 33 mi NE of Concordia, *Hartman et al. 4297* (OS); 41 mi E Mazatlán, hwy 40, *Olsen & Lane 401* (ENCB, LL); Durango hwy at Barranca Liebre, *Ames 77–112* (ARIZ); .4 mi E of La Capilla del Taxte on hwy 40, *La Duke et al. 437** (OS); ca 38 mi E of jct of hwys 40 & 15, *Funk & Canne 3000* (OS).

9b. **Tithonia calva** var. **auriculata** (T. S. Brandegee) La Duke, *comb. et stat. nov.* Figures 46–48.

Gymnolomia auriculata T. S. Brandegee, Zoe **5:** 232. 1905. TYPE: MÉXICO, Sinaloa, Cofradia, Cerro Colorado, 5 Nov 1905, *T. S. Brandegee s.n.* (HOLOTYPE, UC!; ISOTYPES, GH!, POM!, US!).

Tithonia auriculata (T. S. Brandegee) S. F. Blake, Contr. Gray Herb. **54:** 9. 1918.

Stems glabrate to moderately pubescent. Leaves linear to linear-lanceolate, 13–16.5 cm long, 1.1–2.0 cm wide. Receptacle 6–9 mm diam. Disk florets 70–75.

PRINCIPAL FLOWERING TIME: October-December.

DISTRIBUTION: The Mexican states of Sinaloa and Sonora (Fig. 22).

Tithonia calva var. *auriculata* is easily distinguished by its epappose achenes and sessile, linear leaves. Its closest relative is *T. calva* var. *lancifolia* which tends to be similar in leaf morphology, but the ratio between length and width is usually greater than 8 to 1 in the former whereas it is less than 5 to 1 in the latter. Two populations of this taxon have unusual aristate-tipped pales *(La Duke et al. 430; Breedlove 35636),* but agree in all other features with the other populations of this taxon.

REPRESENTATIVE SPECIMENS. MÉXICO. **Sinaloa:** Mesa Malqueson, Cerro Colorado, *Gentry 5144* (MO); 15–20 km E of La Concordia above Copala, *Breedlove 35636* (MICH); 1.1 mi E of Chupaderos on rte 40, *La Duke et al. 430** (OS). **Sonora:** Quirocoba, dist. Álamos, *Gentry 772* (DS, MICH, SMU); Quirocoba, Rio Fuerte, *Gentry 2958* (LL); Sierra Tecurahui SE Sonora, *Gentry et al. 19361* (US).

9c. **Tithonia calva** var. **lancifolia** (B. L. Robinson & J. M. Greenm.) R. McVaugh, Contr. Univ. Michigan Herb. **9:** 443. 1972. Figures 49–51.

Gymnolomia calva var *lancifolia* B. L. Robinson & J. M. Greenm. Proc. Boston Soc. Nat. Hist. **29:** 103. 1899. TYPE: MÉXICO, **Nayarit,** Acaponeta, Feb 1895, *F. H. Lamb 539* (LECTOTYPE here chosen, US!; ISOLECTOTYPES, DS!, GH missing, MO!, NY!, US!). The GH specimen cited by S. F. Blake (1921) was not located (Canoso, *In litt.*).

Tithonia calva subsp. *lancifolia* (B. L. Robinson & Greenm.) S. F. Blake, Contr. U. S. Nat. Herb. **20:** 430. 1921.

Stems sparsely to moderately pubescent. Leaves linear-lanceolate to ovate-lanceolate, 5.7–16.5 cm long, 2.3–4.5 cm wide. Receptacle 7–9 mm diam. Disk florets 60–70 (–130).

PRINCIPAL FLOWERING TIME: January-April.

DISTRIBUTION: The Mexican states of Jalisco, Nayarit, Sinaloa, Sonora (Fig. 22).

Tithonia calva var. *lancifolia* is extremely variable and is most closely related to *T. calva* var. *auriculata,* but some populations

approach the typical variety in many characters. It can be differentiated from *T. calva* var. *auriculata* by its lanceolate leaf shape and flowering time. Populations such as *Argulles 159* and *McVaugh 23555* approach *T. calva* var. *auriculata* most closely in leaf morphology.

REPRESENTATIVE SPECIMENS. MÉXICO. **Jalisco:** Las Mesitas SW of San Sebastian, *Mexia 1893* (BM, DS, F, GH, MICH, MO, NA, NY, UC, US). **Nayarit:** Tepic, *Palmer 1975* (F, GH, MICH, NY, US); 6–12 km NE of Miramar rd to Jalcocotán, *McVaugh 23555* (DS, DUKE, ENCB, LL, MICH, US); km 19, hwy 200, S of Tepic, *Gibson & Gibson 2196* (ARIZ, ENCB, NY, RSA); 17.9 mi W of rte 15 on rd to Jalcocotán, *La Duke et al. 463* (OS). **Sinaloa:** San Ignacio, *Ortega 131* (MEXU); Capadero Sierra Taucuichamona, *Gentry 5543* (ARIZ, DS, GH, MICH, MO, NA, NY). **Sonora:** San Bernardo & vicinity, Curahui, *Arguelles 159* (LL, TEX, US); Sierra Chiribo Río Mayo, *Gentry 1384* (ARIZ, F, GH, MICH, MO, US).

10. **Tithonia longiradiata** (Bertol.) S. F. Blake, Bull. Torrey Bot. Club **53:** 217. 1926. Figures 52–54.

Helianthus longiradiatus Bertol. Novi. Comm. Acad. Sci. Onst. Bonon. **4:** 436. 1840. TYPE: GUATEMALA, **Sacatepequez,** Volcan de Agua, 7 Aug 1962, *G. L. Webster, K. Miller, & L. Miller 12844* (NEOTYPE, MICH!; ISOTYPES, F!, LL!, MO!). The holotype, GUATEMALA, Volcan de Agua, *no collector s.n.* at BOLO was destroyed in the war (D. Ubaldi, *in litt.*). The neotype collection comes from the same locality, is complete in critical features, and is housed in several major herbaria.

Tithonia scaberrima Benth. in Örsted, Viden. Medd. Natur. For. Kjob. 9. 1852. TYPE: NICARAGUA, Segovia, vicinity of Chinotega coniferous region, 5000 ft, Jan 1848, *A. S. Örsted s.n.* (HOLOTYPE, C! [photo, DS!, OS!, US!]; ISOTYPE, C!).

Tithonia platylepis Sch.-Bip. in Benth. & Hook. Gen. Pl. **2:** 368. 1867. *Nom. nud., pro syn.* Based on specimen in "Pl. Lieb. exs." which was not specified.

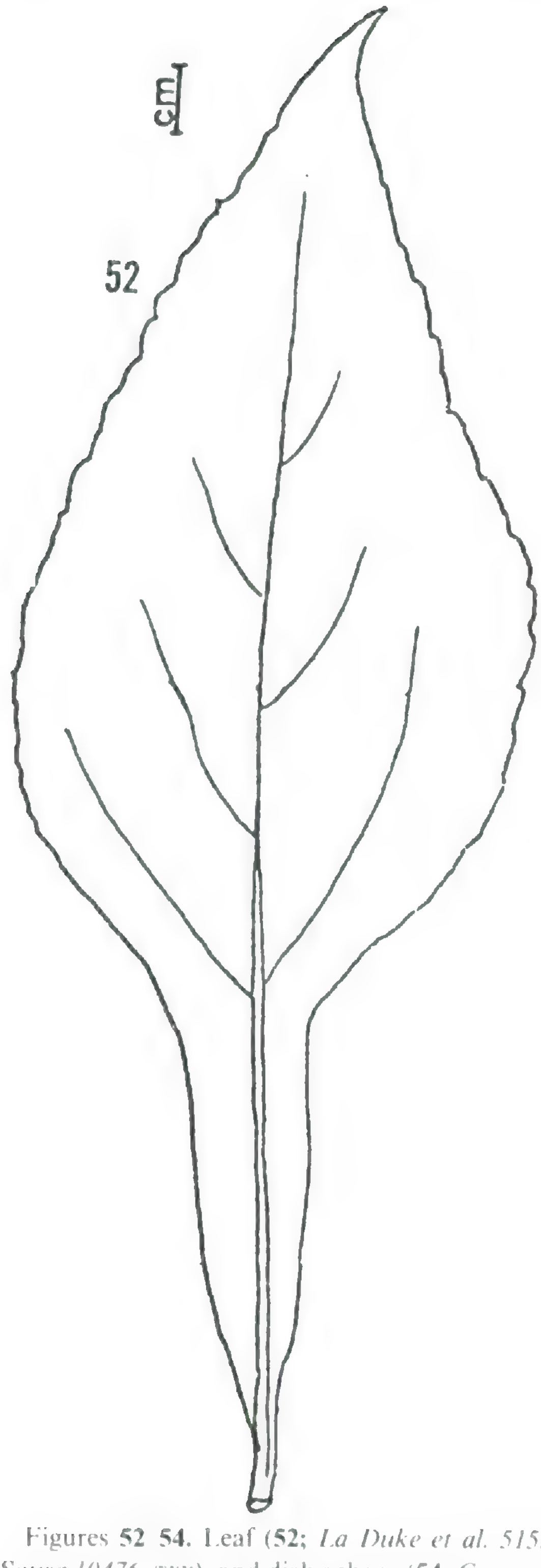
Mirasolia scaberrima (Benth. in Örsted) Benth. & Hook. ex Hemsl. in Godman & Salvin. Biol. Centr. America Bot. **2:** 168. 1881.

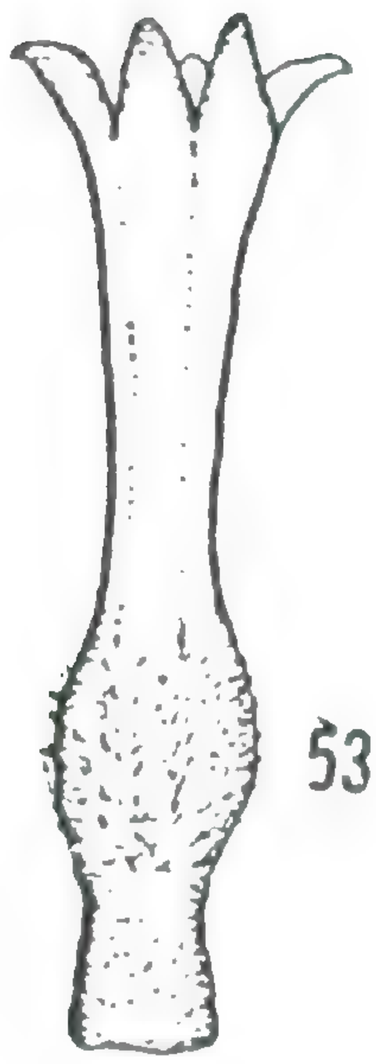
Gymnolomia platylepis (Sch.-Bip.) A. Gray, Proc. Amer. Acad. Arts **19:** 5. 1883. Invalid name, based on *nomen nudum, T. platylepis* Sch.-Bip. in Benth & Hook.

Gymnolomia decurrens Klatt, Leopoldinia **23:** 90. 1899. TYPE: MÉXICO, *C. Sartorius s.n.* (Holotype, not found). *Gymnolomia platylepis* (Sch.-Bip.) A. Gray according to Klatt in a manuscript note (Robinson & Greenman, 1899).

Perimeniopsis perfoliata Sch.-Bip. in Klatt. Leopoldinia **23:** 90. 1899. *Nom. nud., pro syn.* of *Gymnolomia decurrens* Klatt.

Tithonia glaberrima [incorrectly attributed to Hemsl. by] O. Kuntze, Rev. Gen. Pl. **1:** 371. 1891. *Orthogr. var.*





Figures **52**–**54**. Leaf (**52**; *La Duke et al. 515*, OS), disk corolla (**53**; *Cronquist & Sousa 10476*, TEX), and disk achene (**54**; *Cronquist & Sousa 10476*, TEX), of *Tithonia longiradiata*. Figures 53 and 54 same scale.

Gymnolomia pittieri Greenm. Proc. Amer. Acad. Arts **39:** 101. 1903. TYPE: COSTA RICA, "Bords du Rio Ceibo a Buenos Aires," 200 m, Feb. 1891, *H. Pittier 3735*. (LECTOTYPE: GH!, ISOLECTOTYPES, BR!, CR!).

Gymnolomia scaberrima (Benth. in Örsted) Greenm. Field Col. Mus. Publ. **126.** Bot. Ser. **2:** 268. 1907.

Tithonia pittieri (Greenm.) S. F. Blake, Contr. Gray Herb. **54:** 9. 1918.

Erect, perennial, shrub, 1–3 m tall. Stems round, brown to green-brown, pilose to long hispid. Leaves alternate, with petioles to 10 mm long or sessile; blades triangular to ovate to long lanceolate, 8.5–23 cm long, 2.6–13.5 cm wide, at apex acuminate, at base attenuate to truncate, on upper surface scabrous, on lower surface scabrous to pilose, at margin serrate to crenate. Peduncles 2.5–11 cm long, 4–8 mm diam, hispid to villous near head, glabrous lower. Heads solitary, heterogamous. Receptacle 10–14 mm diam. Phyllaries 24–28, four(-five)-seriate, graduated, spathulate; outer bracts 8.5–11 mm long, 3–6.5 mm wide, at apex acuminate, on abaxial surface villous; inner bracts 11–19 mm long, 2.5–6 mm wide, at apex acute to rounded, on abaxial surface minutely hispid. Pales striate, 8–10 mm long, 2–2.5 mm wide; apex acute, 1.5–4 mm long, usually with secondary lobes, minutely pubescent apically. Ray florets 13–30; ligules yellow, oblong, 31–37 mm long, 4.5–8 mm wide, at apex trifid; tube 1.5–2 mm long, 0.75–1 mm diam; pappus absent; achenes one-seriate, white-yellow, sterile. Disk florets 100–200; corollas yellow; corolla lobes 5, 1 mm long, 0.5 mm wide, at apex acute; throat cylindrical with expanded minutely pubescent base, with cylindrical portion 2.5–4 mm long, 1–1.5 mm diam, with expanded portion 0.75–1 mm long, 1–1.5 mm diam; tube minutely pubescent, 0.75–1 mm long, 0.75–1 mm diam; anthers black, 3.5–4.5 mm long; styles 7.5 mm long; stigmas pappillate, 1.5–2.5 mm long; pappus lacking; achenes fertile, black, mottled, rounded quadrangular, 3–4 mm long, 1–2 mm diam, with eliasome at base. Chromosome number, $n = 17$.

PRINCIPAL FLOWERING TIME: November-March.

DISTRIBUTION: Xeric areas of east-central México, south to Panama (Fig. 33).

Tithonia longiradiata is a large shrub most closely related to *T. hondurensis*. It differs in its larger leaves, larger heads, more pubescent peduncle, and non-revolute leaf margin. In some collections

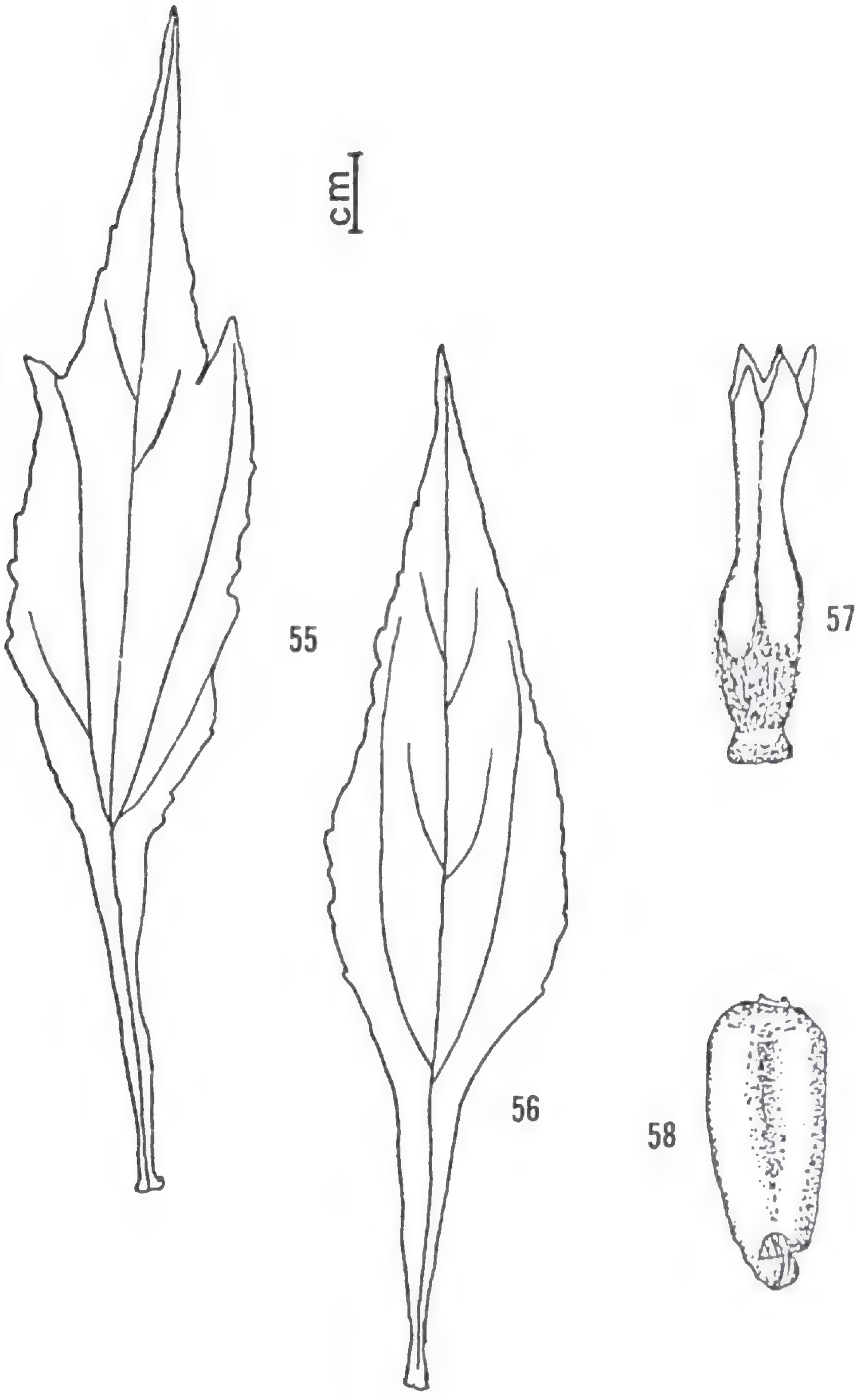
of this taxon only upper leaves were collected and their size approached that of *T. hondurensis* but they lack the characteristic revolute margin of the latter species.

REPRESENTATIVE SPECIMENS. COSTA RICA. **Puntarenas:** Ujarras de Buenos Aires, *Pittier 10631* (CR). EL SALVADOR. **Morazán:** Montes de Cacaguatique, *Tucker 730* (K, LL, MICH, NY, UC, US). **San Vicente:** Volcan de San Vicente, *Standley 21500* (GH, NY, US). GUATEMALA. **Alta Verapaz:** Coban, *Turckheim 2053* (C, F, GH, LL, MICH, MO, NY, US). **Baja Verapaz:** 15 kms N of Salama near Pantin, *Williams et al. 42141* (F). **Chimaltenango:** near Tecpam, *Skutch 718* (DS, GH, LL, MICH, US); 14.6 mi E of 116 km post on rte ca-1, *La Duke et al. 534* (OS). **Guatemala:** 3.5 mi E of San Lucas, rte ca-1, *La Duke et al. 532** (OS). **Huehuetenango:** 24 mi NW Huehuetenango rte ca-1, *La Duke et al. 536* (OS). **Peten:** La Libertad, *Aguilar 472* (MICH, MO, NA, US). **Progreso:** Zanarate and El Chato bridge, *Molina and Molina 24926* (F, NY, US). **Queretaro:** rte 95, ca 10 mi S Quezaltenango, *King 3428* (DS, MICH, NY, TEX, US). **Quezaltenango:** Volcan Santa Maria de Jesús, hwy 95, *Stuessy & Gardner 4340* (OS). **Quiche:** Nebaj, *Skutch 1886* (F, GH, LL, NY, US). **Sacatepequez:** slopes of Volcan de Agua S of Santa Maria de Jesús, *Standley 59434* (F). **San Marcos:** S of San Marcos toward Castalia, *Williams et al. 26162* (F). **Solola:** San Lucas, 24 Jan 1907, *Kellerman sn* (OS). HONDURAS. **Copan:** between land de La Puerta & El Salto, *Pittier 1854* (F, US). **El Paraiso:** trail Danli to Finca La Enllia, *Carlson 2567* (F, MICH, UC). **Morazán:** entre Pena Blanca y lo de Ponce, *Williams & Molina 17109* (GH).

MÉXICO. **Chiapas:** S of Nicolas Montecristo, *Matuda 1957* (F, GH, MEXU, MICH, MO, NY, US); 8 mi W of San Cristobal de las Casas, *Cronquist & Sousa 10476* (DS, DUKE, ENCB, GH, MICH, NY, TEX, US); Tenejapa, *Ton 570* (DS, ENCB, GH, LL, NY); 3.7 mi E of rd to Apaz on rt 190, *La Duke et al. 515** (OS); 4.1 mi S Trinitaria, rte 190, *La Duke et al. 537* (OS). **Hidalgo:** Chalpulhuacan, *Cottam 10525* (ARIZ); rte 85, 5 mi SW of Hidalgo San Luîs Potosî border, *King 4232* (F, MICH, NY, TEX, UC, US). **Oaxaca:** vicinity of Totentepec, *Nelson 772* (US). **Puebla:** km 8 de la Carr, que Baja a la Mina el Paraiso v Juarez, *Sarukhan et al. 1218* (MEXU). **San Luîs Potosî:** mtns along rt 120 about 6 mi W of Xilitla, *King 4435* (MICH, NY, TEX, UC, USF). **Veracruz:** Fortin, *Kerber 327* (C, MICH, US); hill of Borregolorizaba, *Pringle 6087* (GH, MEXU, MO, NA, NY, UC, US); Zacuapam, *Purpus 2183* (F, GH, MO, NY, UC, US); El Durzano, San Juan Coscomatepec, *Ventura 4863* (DS, ENCB, MICH, RSA, TEX). NICARAGUA. **Jinotega:** vicinity of Jinotega, *Standley 9882A* (F).

11. **Tithonia hondurensis** La Duke Rhodora **84:** 139. 1982. TYPE: HONDURAS, **El Paraiso,** 5 mi W of dirt rd to Ojo de Agua and highway from Danli to Zamorano (hwy 4), 4 Dec 1978, *V. A. Funk, K. Landon 2938** (HOLOTYPE, OS!; ISOTYPE, F!, NY!). Figures 55–58.

Erect, perennial, shrub, 0.5 -4 m tall. Stems round, tan to brown, moderately hispid to glabrous. Leaves alternate, sessile or with petioles to 4 mm long; blades linear to linear-lanceolate, occasionally



Figures **55–58.** Leaves (**55** & **56**), disk corolla (**57**), and disk achene (**58**) of *Tithonia hondurensis* (*Funk & Landon 2938*, OS). Figures 57 and 58 same scale.

with two small lobes at base, 6.5–23 cm long, 1.5–2.8 cm wide, at apex acuminate, at base attenuate to rounded attenuate, on upper surface short pubescence, densely puberulent, on lower surface longer, tomentose, at margin entire to serrate or crenate, revolute. Peduncles 8.5 25 cm long, 3 7 mm diam, sparsely to moderately hispid near head, reduced below. Heads usually solitary, heterogamous. Receptacle 10 15 mm diam. Phyllaries 20 23, four-seriate, graduated, linear to spathulate; outer bracts 4.5–8 mm long, 2 4 mm wide, at apex rounded, on abaxial surface slightly puberulent; inner bracts 7 11 mm long, 2 4 mm wide, at apex rounded, on abaxial surface glabrous. Pales striate, 6.5 9 mm long, 0.75 2 mm wide; apex acute, 0.5 1 mm long, with or without lateral lobes, minutely pubescent apically. Ray florets 13 15, neuter; ligules yellow, linear to ovate, 18 42 mm long, 6 10 mm wide, at apex trifid; tube 1 1.5 mm long, 0.5 .75 mm diam; pappus absent; achenes one-seriate, triangular, white. Disk florets 60 80; corollas yellow; corolla lobes 5, 0.75 1 mm long, 0.5 mm wide, at apex acute; throat cylindrical with expanded minutely pubescent base, cylindrical portion 2.5 3 mm long, 0.75 1 mm diam, expanded portion 1 2 mm long, 1 mm diam; tube minutely pubescent, 0.5 1 mm long, 0.5–.75 mm diam; anthers black, 3 4 mm long; style 5.75 7 mm long; stigmas pappillate, 1.5 1.75 mm long; pappus lacking; achenes fertile, black, rounded quadrangular, 3.5 mm long, 1.5 mm diam, with eliasome at base. Chromosome number, $n = 17$.

PRINCIPAL FLOWERING TIME: November-March.

DISTRIBUTION: Belize and Honduras (Fig. 59).

Tithonia honduresis is a small shrub distributed locally in Belize Honduras and Honduras. It can be recognized easily by its small heads (receptacle 10 15 mm diam), and revolute leaf margins. Its closest relative is *T. longiradiata* from which it is distinguished by the above mentioned characteristics. This taxon has not been extensively collected, but the known range of morphological variation is quite great. Populations in Belize have the largest plants in all characters (e.g., *Spellman 1412*), while populations near Sigatepeque, Honduras are much smaller (e.g., *Molina 23298*). Characters of the secondary branches are also smaller than those on the main stem.

REPRESENTATIVE SPECIMENS. BELIZE. **Cayo:** *Hunt 295* (LL, BM); Makal River at end of Kinloch rd, *Spellman 1412* (MO). Vaca Falls: 1926, *Record sn* (OS). HONDURAS.

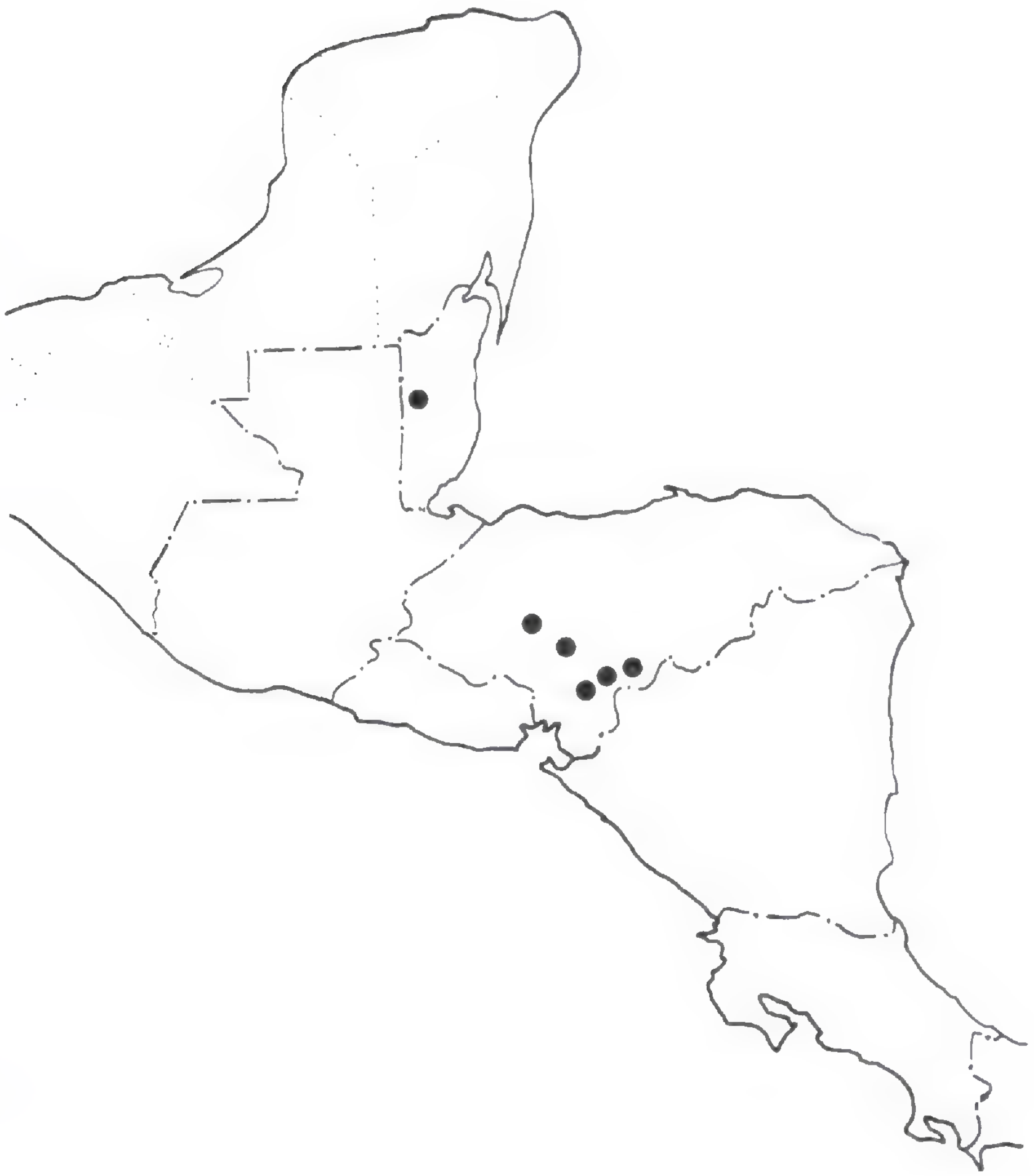


Figure **59**. Distribution of *Tithonia hondurensis* in Central America.

Comayagua: 3 km S of Siguqtepeque, *Molina 23298* (F, MO, NY, US); ca. 20 mi SE Comayagua on rte 1, *Stuessy & Gardner 4420** (OS). **El Paraiso:** Manzaragua rd, *Williams 11497* (F, GH, MEXU); Quebrada de Dantas on rd btwn Las Mesas & Yuscaran, *Standley 14984* (F); 8 km W of Ojo de Agua, *Williams 14750* (F); 8 km N of Yuscaran, *Williams & Williams 18655* (F, GH, LL, US); NE of Danli, *Molina 7599* (F); in Pine Forest of Guayabillas Road to Ojo de Agua, *Molina 25904* (DUKE, F, MO, NY, US).

DOUBTFUL AND EXCLUDED TAXA

Tithonia angustifolia Hook. & Arn. Botany Beechy Voyage 435. 1841. TYPE: MÉXICO, **Nayarit,** between San Blas and Tepic, *A.*

Sinclair s.n. (Holotype, K [photo, F!]). =*Viguiera angustifolia* (Hook. & Arn.) S. F. Blake, Proc. Amer. Acad. Arts **19:** 5. 1883.

Tithonia agrophylla D. C. Eaton in S. Watson, U.S. Geol. Exp. 40th Par. Bot. **5:** 423. 1871. TYPE: Location and date unknown, *E. Palmer s.n.* (HOLOTYPE, YU! on two sheets; ISOTYPE US!). =*Enceliopsis agrophylla* (D. C. Eaton in S. Watson) A. Nelson, Bot. Gaz. **47:** 433. 1909.

Tithonia decurrens A. Gray, Mem. Amer. Acad. Arts. Ser. 2. **4:** 85. 1849. TYPE: MÉXICO, **Chihuahua,** on the Bufa, Oct, *F. A. Wislizenus 193.* (HOLOTYPE, GH!). =*Viguiera decurrens* (A. Gray) A. Gray, Proc. Amer. Acad. Arts **19:** 5. 1883.

Tithonia excelsa (Willd.) DC. Prodr. **5:** 585. 1836. =*Helianthus excelsus* Willd. Sp. Pl. **3:** 2243. 1804. TYPE: location, date and collector unknown (HOLOTYPE, not found) =*Viguiera excelsa* (Willd.) B. & H. ex Hemsl. Biol. Centr. Amer. **2:** 177. 1881, fide Blake (1918). Identity based on plate 219 of *H. giganteus* Cav. Icon. **3:**10. 1795 which is a later homonym.

Tithonia glutinosa Hook. & Arn. Botany Beechy Voyage. 33. 1841. *pro. syn., nom. nud.*

Tithonia humilis (L.) O. Kuntze, Rev. Gen. Pl. **2:** 552. 1891. =*Rivina humilis* L. Gen. Pl. **1:** 121. 1753.

Tithonia ovata Hook. Bot. Mag. *t. 3901.* 1841. TYPE: MÉXICO, cultivated at Kew Gardens. (HOLOTYPE, K). =*Lasianthaea helianthoides* DC. Prodr. **5:** 608. 1836. Identification made from figure (*t. 3901*), and confirmed by Becker (1977).

Tithonia pachycephala DC. Prodr. **5:** 585. 1836. TYPE: MÉXICO, Guanajuato, 1829, *Mendez s.n.* (HOLOTYPE, G-DC, IDC *800, 949:* I. 1!, Photo F!). =*Viguiera pachycephala* (DC) Hemsl. Biol. Centr. Amer. Bot. **2:** 178. 1881.

Tithonia pusilla A. Gray, Proc. Amer. Acad. Arts **5:** 124. 1861. TYPE: PERU, Obrajillo, *W. Rich s.n.* (HOLOTYPE, GH; ISOTYPE, US!). =*Viguiera pusilla* (A. Gray) S. F. Blake, Contr. Gray Herb. **54:** 162. 1918.

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STATUS AND IDENTIFICATION OF HYDROCHARIS MORSUS-RANAE AND LIMNOBIUM SPONGIA (HYDROCHARITACEAE) IN NORTHEASTERN NORTH AMERICA

P. M. CATLING AND W. G. DORE

Abstract. Since 1939, when it escaped into the Rideau canal at Ottawa, *Hydrocharis morsus-ranae* has spread throughout much of southeastern Ontario, southern Quebec, and northern New York State. Over the past fourteen years it has increased its area of occurrence in North America by three times and is now known throughout the Rideau canal system, the lower Ottawa River, the entire St. Lawrence, eastern Lake Ontario, and also at Rondeau Park on the north shore of Lake Erie. It has also become much more frequent in areas from which it has been known for 10–20 years. Occurrence in isolated pools suggests effective dispersal and colonization which may involve both seeds and turions. Although *H. morsus-ranae* differs from most other North American aquatics in having very rounded leaves with five prominent and converging primary veins, these characters do not distinguish it from floating-leaved forms of *Limnobium spongia*. The recent spread of *H. morsus-ranae* has resulted in it closely approaching the range of *L. spongia*, although the present distribution of the latter does not extend north of Illinois in the Mississippi drainage or north of New Jersey on the Atlantic coastal plain. *Hydrocharis morsus-ranae* differs from *L. spongia* in having relatively less well developed aerenchyma on the undersurface of the leaf, relatively longer leaf lobes, leaf veins on either side of the midvein less ascending, free stipules in pairs, roots usually unbranched and stolon buds developing one instead of numerous roots initially. Other characters differing between the two taxa are described including flowers, seeds, petiole lengths, and leaf venation. These latter characters are less significant in identification either due to their frequent absence on collected material or qualitative and overlapping nature.

The European Frog-bit, *Hydrocharis morsus-ranae* L., was planted in ponds beside Dow's Lake in the Central Experimental farm arboretum at Ottawa in 1932. By 1939 it had spread to the adjacent Rideau Canal (Minshall, 1940). By 1953 masses were noticed free-floating in the Rideau Canal and it was discovered on the Ottawa River near Cumberland, 21 km to the east (Dore, 1954). Also in 1953 it was found floating on Riviere des Mille-Iles near the confluence of the Ottawa and the St. Lawrence Rivers. These plants may have come from stock established at Ottawa or may have escaped from the Montreal Botanical Garden where it was also cultivated. By 1967 *H. morsus-ranae* had been found along the Ottawa River between Ottawa and Montreal and on the St. Lawrence River from Montreal as far as Lake St. Peter (Louis-Marie, 1958, 1960,

1961, 1962; Dore, 1968a,b). The distribution of *H. morsus-ranae* in Quebec was shown by Joyal (1970). In addition it had been found at numerous localities from Merrickville on the Rideau River to the confluence of the Rideau and Ottawa Rivers (Dore, 1968a,b). The total extent of its North American occurrence at this time was a stretch of major waterways approximately 340km in length. It occurred primarily in marshy bays but was often seen free-floating downstream.

Since 1967 it has been found at several localities substantially outside this area, suggesting a rapid spread (Reddoch, 1976; Roberts et al., 1981). The status of *H. morsus-ranae* up to 1967 was outlined in detail by Dore (1968a,b).

The recent spread of *H. morsus-ranae* has resulted in increased opportunities for confusion with native species, especially with the North American Frog-bit, *Limnobium spongia* (Bosc.) Steud. Since *H. morsus-ranae* is a relatively recent European introduction and did not occur near to the neartic *L. spongia*, very few authors have compared the two taxa and there are no detailed comparisons. The only readily available key including both species is that of Scoggan (1978) which is difficult to use and often fails to separate them correctly. The purpose of this article therefore is to update information on the status and distribution of these two taxa in northeastern North America and also to present the results of a comparative morphological study indicating salient differences.

METHODS

Specimens of *Hydrocharis morsus-ranae* and *Limnobium spongia* from several northeastern herbaria (CAN, DAO, GH, NYS OAC, SFS, TRT) were examined. These specimens provided the basis for mapping of distribution and for morphological comparison. In addition to specimen records, an indication of status and distribution was obtained through communication with herbarium curators and field botanists.

Herbarium specimens of *Limnobium spongia* from the southeastern United States, *Hydrocharis morsus-ranae* from Canada and *H. morsus-ranae* from Europe were selected for recording of character states and measurement. They were selected to cover a broad geographical area within each of the above regions and also so as to avoid measuring more than two plants from a single locality. Three measurements were made and character states recorded on one or

two separate rosettes per sheet. In this way 49 sets of measurements were taken from 26 sheets of *L. spongia*, witih no more than two sets of measurements being made per sheet. Similarly 31 sheets of *H. morsus-ranae* from Europe resulted in 55 sets of measurements and 24 sheets of *H. morsus-ranae* from Canada gave 46 sets of measurements. Label data were recorded for each sheet and the three characters (including maximum aerenchyma space diameter, leaf length, and leaf lobe length) were measured using a scale marked in tenths of a mm. The states of various other characters were noted (*i.e.* approximate angle of primary lateral vein divergence, presence of branching roots, number and attachment of stipules, number of stolon bud roots, and presence or absence of flowers and fruit).

The leaves chosen for measurement were generally selected to include the apparent range of variation (on the sheet) in the characters measured. Frequently this criterion could not be applied due to backmounting, folded leaves or damage, with the result that only one or two leaves were measurable.

The maximum aerenchyma space diameter is defined as the maximum diameter of an aerenchyma space (*i.e.* a space in the lacunate mesophyll) in the basal portion of the leaf between the midvein and the first primary lateral vein (Figure 1). In an attempt to standardize this measurement, it was determined that the space selected for measurement had to be at least 2 mm above the point where the veins diverge and 1 mm from the midvein. The measurement of leaf length and leaf lobe length is illustrated in Figure 1.

The ranges, means, standard errors, and standard deviations were recorded for characters measured. In addition, leaf lobe length was expressed as a ratio of leaf length to determine the extent to which *H. morsus-ranae* has proportionately longer basal lobes. Other distinctive features were recorded in tracings, camera lucida drawings, or photographs.

RECENT SPREAD OF HYDROCHARIS MORSUS-RANAE

(a) St. Lawrence River region

In 1970, botanists at Queen's University found *Hydrocharis morsus-ranae* at two locations in the St. Lawrence River below Rockport in Leeds County (A. E. Garwood, pers. comm., Table 1). In 1972 it was observed to be locally abundant in the cattail (*Typha* spp.) marsh surrounding the bays around Squaw, Adelaide, and

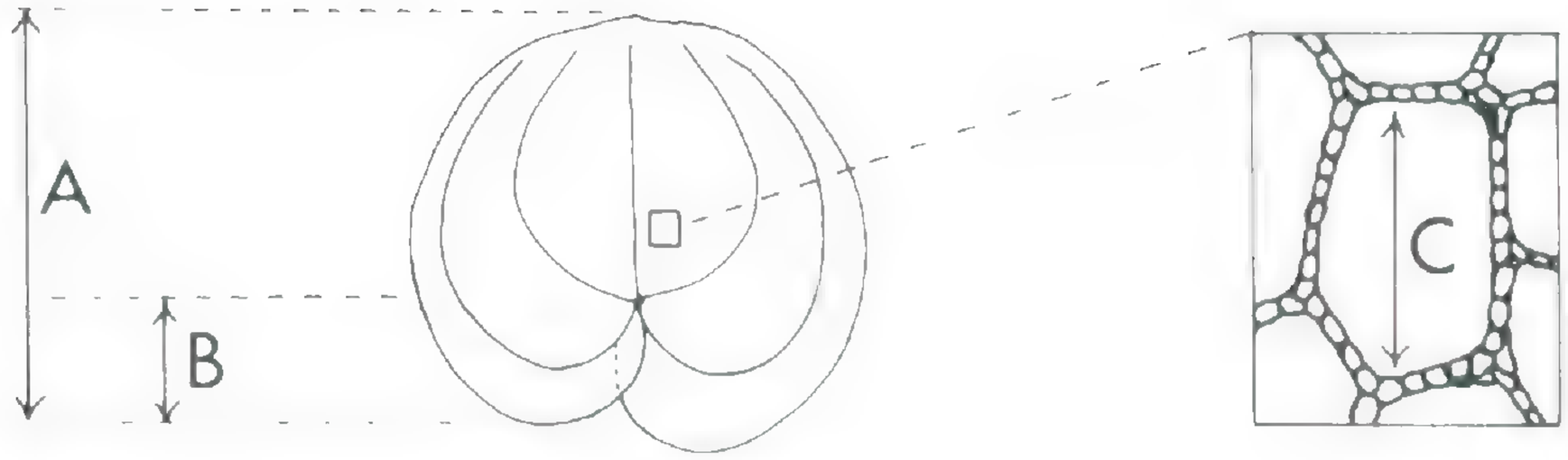

Figure 1. Method of measurement of leaf length (A), leaf lobe length (B) and maximum aerenchyma space diameter (C).

Grenadier Islands and it was recorded from this area in a subsequent floristic survey (Cody, 1975). In 1974 *Hydrocharis morsus-ranae* was discovered in the Lake St. Francis area lower down the St. Lawrence, at South Lancaster, Glengarry Co., Ontario and at Ogdensburg in St. Lawrence Co., New York (Table 1). Subsequently it was discovered at other nearby localities in New York State (Table 1, Roberts et. al., 1981).

In addition *H. morsus-ranae* has extended down the St. Lawrence River to Quebec City (Table 1), about 124 km beyond its 1967 limit shown by Dore (1968a,b) and its 1970 limit shown by Joyal (1970).

(b) Rideau Canal and Ottawa systems

Confined to sections of the Ottawa River downstream from Ottawa in 1967, *H. morsus-ranae* has extended upstream to Shirleys Bay (D.F. Brunton, 1981, Ecological inventory of the Shirleys Bay study area, Ottawa-Carleton, Ontario, National Capital Commission), to the Constance Bay area (P.M. Catling, pers. obs.), and further upstream to Lavergne Bay, Morris Island, near Arnprior, ca. 50 km upstream fro Ottawa (A. H. Reddoch, pers. comm., Table 1) and to Fort Coulonge, ca. 100 km upstream (Table 1). In 1975 it was collected at Lake Opinicon along the Rideau Canal (Table 1) ca. 55 km to the southwest of the limit established by Dore in 1968.

(c) Lake Ontario

In 1972 *H. morsus-ranae* was found in the Bay of Quinte near Rossmore, Prince Edward County. It was discovered at another location ca. 40 km to the west near Deseronto, also in the Bay of Quinte in 1974. In 1977 it was found in Presqu'Ile Bay, an embayment of Lake Ontario near Brighton in Northumberland County (Table 1).

Table 1.
Specimen citations for *Hydrocharis morsus-ranae*
collected in North America beyond the range
indicated by Dore (1968).

CANADA
Ontario

FRONTENAC CO.: creek running under Lake Opinicon Rd., 3 miles from Perth Rd. (east of Cambells farm (44°37′ N.L., 76°18′ W.L.), 6 Aug. 1975. *A. Kitces* (OAC).

STORMONT, DUNDAS AND GLENGARRY CO.: Forming dense floating mats on water less than 3 feet deep, in a small marshy boat-channel along the northwest side of the "Lake St. Francis" section of the St. Lawrence River, South Lancaster, Ontario, 12 September 1974, *F. M. Uhler* (NYS).

HASTINGS CO.: Bay of Quinte, Deseronto, 1974, *G. Miller* (OAC).

KENT CO.: Rare, drainage channel, Rondeau Provincial Park, 23 June 1976, *H. Dale and J. Gerrath* (OAC); abundant North channels, Rondeau Park, 1978, *E. Woodley* (herb. H. M. Dale, n.s.); very abundant, dominant, Rondeau Park, 1980, *H. Dale* and *V. Posluszny* (herb H. M. Dale, *n.s.*).

LEEDS AND GRENVILLE CO.: Squaw Island in St. Lawrence about 4 miles below Rockport, tangled among *Typha* plants in still water and lagoon; (plant first detected here in 1970 by A.E. Garwood and M. Good, specimen QK*96127 1971, W. G. Dore et al 24845* (DAO); water and reeds, Squaw Island, Front of Yonge Township, 28 July 1972, *J. G. Woods 43* (DAO); Adelaide Island, F. of L. & L. Twp., reeds, still water, much duckweed, 28 July 1972, *J. G. Woods 44* (DAO). Squaw Island (about 4 miles below Rockport) in St. Lawrence River, 11 July 1973, *W. G. Dore et al 25118* (DAO); Squaw Island, 44°25′ N., 75°52′33″. W., drying up depression in marsh, 17 June 1975, *W. J. Cody & D. Munro 21871* (DAO); Squaw Island 44°25′N. 75°52′3″W., in *Typha* marsh, 17 June 1975, *W. J. Cody and D. Munro 21885* (DAO); Grenadier Island East, 44°26′ N., 75°51′ W., wet ditches, 19 June 1975, *W. J. Cody and D. Munro 21996* (DAO); Adelaide Island in Thousand Islands archipelago of St. Lawrence River among cattails and shallow water vegetation, 10 August 1976, *W. G. Dore, A. Crowder, S. Vander Kloet and A. Garwood 24848* (DAO); shal-

low, marshy water of middle Kemptville Creek, 4 miles sw of Bishops Mills, 27 July 1979, *W. G. Dore* (DAO).

OTTAWA-CARLETON, REG. MUNIC.: Lavergne Bay on Ottawa River ca. 5 miles east of Arnprior on Morris Island, 11 Aug. 1969, *A. H. Reddoch and J. M. Reddoch* (DAO).

NORTHUMBERLAND CO.: Shallow water in bay, Presqu'ile Bay, a few miles south of Brighton, just outside Presqu'ile Provincial Park, Brighton Tp, 44°00′ N., 77°43.5′ W., 23 July 1977, *P. M. Catling, et al.* (DAO, TRT).

PRINCE EDWARD CO.: growing at edge of *Typha* marsh, Ameliasburg, 23 July 1972, *S. Vander Kloet* (QK); Hennesey Point (Rossmore) along creek channel 60-120 cm deep, substrate –sedge peat, 23 July 1972, *S. Vander Kloet and M. R. King* (QK, OAC); growing in a few cm of water in thick stands among bases of *Typha*, around Deseronto, 29 July 1974, *G. Miller* (OAC).

Quebec

PONTIAC CO.: dans un étange, Fort-Coulonge, 27 juillet 1979, *N. Lesage 1391* (SFS).

QUEBEC CO.: marécage du camp Maizerets, 4 août 1974, 3 août 1978, *J. St.-Pierre 76 and 120* (SFS).

UNITED STATES

New York

JEFFERSON CO.: Kring Point, Kring Point State Park, shore of the St. Lawrence River in a small bay ca. 10 miles east of Alexandria Bay. Abundant in bay in 2-3 feet of water on mucky bottom, 20 September 1979, *M. L. Roberts 5133* (NYS; duplicates at OS, DH *n.v.*)

ST. LAWRENCE CO.: small bay along the west side of the Oswegatchie River, just south of Ogdensburg, 13 September 1974, *F. M. Uhler* (NYS); 1.2 miles north of highway 11 on the road to Rensselear Falls, 15 June 1977, *R. S. Mitchell and J. K. Dean 6032* (NYS): open marsh on highway 68, 5.8 k north of Canton, 9 May 1981, *P. M. Catling 3120* (DAO, MICH, NYS, OS).

(d) Lake Erie

Hydrocharis morsus-ranae was found in Rondeau Park on the north shore of Lake Erie, Kent County, in 1976 (Table 1). It was noted as "rare' in 1976 at the site, but "abundant" in 1978, and "very abundant, dominant" in 1980 (H.M. Dale, pers. comm., Table 1).

The new discoveries of *H. morsus-ranae* described above suggest that it has increased its area of occurrence in North America by about three times over the past 14 years (Figure 2.).

Local increases

In addition to spreading outside the area from which it was known in 1967, *H. morsus-ranae* has become much more abundant and frequent within this area of 1967 occurrence, the lower Rideau and lower Ottawa watersheds. It is now present in numerous locations where it was unknown previously according to the carefully compiled field records of absence. Some of these locations are roadside ditches, ponds, and marshy pools created by beaver dams along small creeks, all largely isolated from the major rivers (Ottawa, St. Lawrence, Rideau) to which *Hydrocharis* was initially confined. Similarly it has been found at additional locations in the St. Lawrence system downstream from Montreal, suggesting that it has increased in this area as well (S.G. Hay, pers. comm.).

Hydrocharis morsus-ranae usually occurs in water of pH 6.5–7.8 with cattails (*Typha* spp.) and duckweed (*Lemna minor*) in areas that are apparently nutrient-rich. These conditions are widespread, except in parts of the Canadian Shield region, and habitat requirements seem unlikely to limit its further spread in North America.

DISPERSAL OF HYDROCHARIS MORSUS-RANAE

Hydrocharis morsus-ranae may be rooted in mud or lodged in shoreline debris or it may be free-floating. Any free-floating aquatic may be effectively spread by the natural flow and circulation of water. The initial spread of *H. morsus-ranae* was essentially downstream (with the exception of a canal; Dore, 1968a) and it seems likely that dispersal by water played a significant role.

Hydrocharis morsus-ranae reproduces vegetatively and overwinters through the development of turions (modified stolon buds around which the scales remain tightly clasped). These turions separate from the parent plant by abscission in late fall, sink to the bottom where they overwinter, and rise to the surface in the following spring to start new plants (pers. obs.: Ridley, 1930, p. 184; Sculthorpe, 1967, p. 350; Dore, 1968a). The characteristic occurrence of stolon buds and turions, which represent relatively small vegetative reproductive parts (ca. 1 cm long) on almost all plants

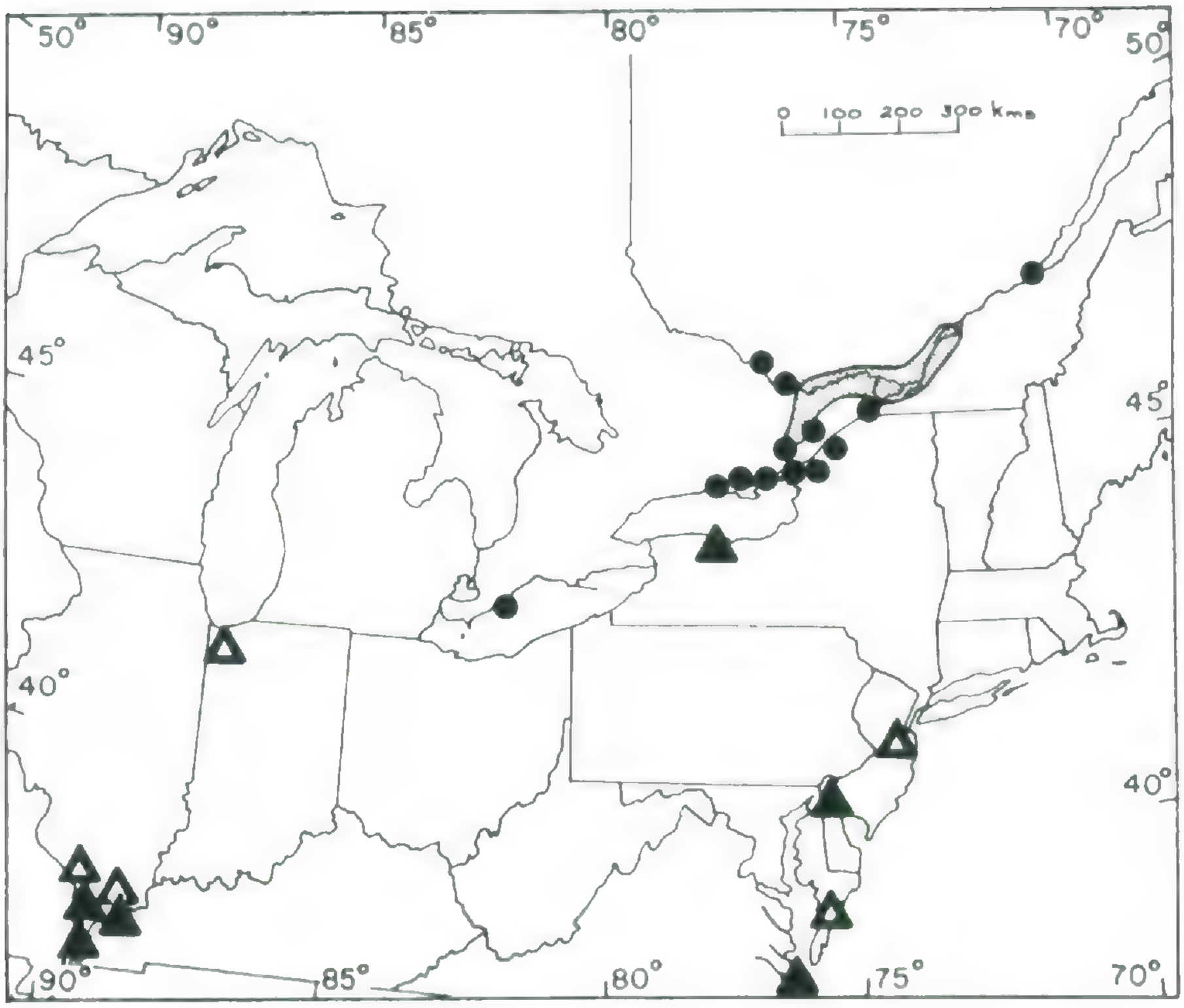

Figure 2. Map of a southwestern portion of northeastern North America showing the distribution of *H. morsus-ranae* (shaded area = to 1967, dots = from 1968 – 1981) and *L. spongia* (solid triangles = specimens seen, open triangles = literature reports (specimens not seen)).

encountered, greatly increases the likelihood of dispersal and establishment. Parts of plants, including stolon buds or turions, may be carried by boats on anchors and ropes. Plant parts may also be carried by waterfowl over considerable distances by lodging in the feet or bill. Several gullets from Black Ducks (*Anas rubripes*) collected during the autumn of 1971 on the Ottawa River near Thurso, Quebec and Wendover, Ontario, were found to contain the turions of *H. morsus-ranae* (F.H. Uhler, pers. comm.). Whether or not these turions would come out of the ducks alive and capable of growth is unknown.

Turions are very important in the establishment and persistence of *Hydrocharis morsus-ranae*. Flowering is irregular and the plants are dioecious and some colonies are of one sex so that seed production is limited. Weber (1972) has indicated the importance of turions in the propagation of *Myriophyllum exalbescens*. In his Douglas Lake (Michigan) study area most of the plants present had devel-

oped from turions and most produced turions with an average of more than one turion per plant. Similarly, it appears that most North American colonies of *H. morsus-ranae* develop from overwintering turions and that most populations also produce turions abundantly. At three stations near Ottawa and one near Ogdensburg in New York State, each having hundreds of plants, the entire colonies in 1981 developed from overwintering turions, there being no evidence of germinating seed.

There is a possibility that some colonies of *Hydrocharis morsus-renae* have been started either intentionally or accidentally by humans. Some duck hunting clubs introduce aquatic plants intentionally from other regions in order to provide food and cover for waterfowl. People frequently take aquatic plants into an aquarium with fish, salamanders, and turtles, and later release the entire contents (including aquatic plants) into an environment removed some distance from the point of origin.

Although *Hydrocharis morsus-ranae* is dioecious, plants of different sexes sometimes occur abundantly together (Dore, 1968a) and capsules ripen with seed (*e.g.:* Ste. Anne de Bellevue, 28 Aug. 1961, *D. E. Swales* (DAO). Ridley (1930, pp. 538, 621) discusses the possibility of dispersal of *H. morsus-ranae* by adhesion of the seeds to waterfowl (due to the viscid exudation with which they are surrounded). McAtee (1939; see also Ridley, 1930, p. 491) reports that the seeds of *Limnobium spongia* (a species closely related to *H. morsus-ranae* and with very similar seeds) may represent an important duck food. They have been identified in the stomachs of several species of ducks, with 32,000 being found in a single bird. The extent to which the seed of *H. morsus-ranae* and *L. spongia* are capable of passing through the digestive tracts of waterfowl without damage is unknown.

DISTRIBUTION AND STATUS OF LIMNOBIUM SPONGIA IN NORTHEASTERN NORTH AMERICA

The distribution of *Limnobium spongia* in northeastern North America is shown in Figure 2. It occurs on the Atlantic coastal plain from New Jersey southward and in the Mississippi drainage from southern Illinois southward, with disjunct stations reported in Monroe Co., New York and Lake Co., Indiana.

References to the occurrence of *Limnobium spongia* in Ontario

(Taylor, 1915; Small, 1933) are erroneous and apparently based on previously recorded occurrences in "Lake Ontario" (*e.g.:* Britton, 1901; Britton and Brown, 1913; Robinson and Fernald, 1908). All references to "Lake Ontario" refer to the station at Braddock's Bay, Greece, in Monroe County, New York (Paine, 1865; House, 1924). There are correctly identified specimens to document this occurrence (Table 2) collected in 1828. By 1895 it was noted that *L. spongia* had "not been seen for several years" at Braddock Bay (House, 1924). Clausen (1940) surveyed Braddock Bay but did not find *L. spongia*. More recently it has been reported to be "probably extinct" in Monroe Co. (e.g. Fernald, 1950). There are apparently no recent observations of *L. spongia* in the Braddock Bay area (H.S. Forest, pers. comm.).

The literature report from Lake County, Indiana (Deam, 1940) is apparently not supported by material evidence (F.A. Swink, pers. comm.).

IDENTIFICATION OF HYDROCHARIS MORSUS-RANAE AND LIMNOBIUM SPONGIA

A number of North American aquatic genera may have wide floating leaves with cordate bases (i.e. *Alisma, Caltha, Echinodorus, Heteranthera, Nuphar, Nymphaea, Nymphoides, Ottellia, Polygonum, Potamogeton,* and *Sagittaria*), but only two genera have leaves that combine: more or less circular shape, rounded lobes, more or less rounded apex and five pronounced and converging primary veins. These latter features are shared by the genera *Hydrocharis* and *Limnobium.*

Louis-Marie (1959) noted that *Hydrocharis morsus-ranae* and *Limnobium spongia* may resemble one another very closely, but that the floral structures are quite different. Cook, et al. (1974), in their work on aquatic plant genera, also concentrated on flowers, indicating that *Limnobium* spp. are either without petals or with petals less than 1½ times as long as the sepals, whereas *Hydrocharis* spp. have petals more than 1½ times as long as the sepals. This latter distinction is a very useful one (Figure 3).

The staminate flowers of *Hydrocharis morsus-ranae* have 9–12 stamens with relatively long free filaments not obviously connate at the base, and with the free portion as long as the anthers. In contrast, *Limnobium spongia* has 3–12 stamens with filaments largely

Table 2. **Specimen citations for *Limnobium spongia*** in northeastern North America.

UNITED STATES

Delaware

NEW CASTLE CO.: In ditches along canal, Delaware City, 11 September 1871, *A. Commons* (2 sheets, NY); in stagnant ditches near Delaware City, September 1, 1880, *A. Commons* (GH, NY); margin of lagoon, ¾ mile southwest of Delaware City along road to St. Georges, 13 July 1937, *R. R. Tatnall 3439* (GH).

Kentucky

BALLARD CO.: Floating with *Lemna* in Bald Cypress swamp, Peal Wildlife Management area, 3 km west of Barlow, 23 April 1981, *P. M. Catling 3907 and K. L. Catling* (DAO).

Illinois

UNION CO.: Jonesboro, August 1862, *G. Vasey* (GH); Jonesboro, *G. Vasey* (NY); southern Illinois, *G. Vasey* (GH).

Missouri

MISSISSIPPI CO.: Margin of muddy shallow bank of Big Lake ditch No. 1 along road N, just north of junctionwith road K, T27N, R16E, sect. 30 2½ miles (by air) north of Charleston, 21 August 1955, *J. A. Steyermark 79593* (GH).

New York

MONROE CO.: growing in stagnant water, surrounded with *Azolla*, on the shore of Lake Ontario in the town of Greece, 21 April 1828, *Bradley* (NY - Torrey herbarium and label in Torrey's hand; photo DAO); Braddocks Bay, Lake Ontario, *H.P. Sartwell* (GH); north shore of Braddock's Bay, Greece, Herbarium *Wm. Boott* (GH).

Virginia

NORFOLK CO.: Sandy and peaty margin of Lake Drummond, near Jericho ditch, Great Dismal Swamp west of Wallaceton, 6 September 1941, *M. L. Fernald and Bayard Long 13519* (NYS, GH); wooded river-swamp along Northwest River, northeast of Northwest, 17 October 1941, *M. L. Fernald and B. Long 13861* (GH).

PRINCESS ANNE CO.: In water of cove, southern end of Lake Joyce, 12 September 1935, *M. L. Fernald et al 4744* (GH, NY); on water margin of Lake Joyce, 4 May 1935, *M. L. Fernald and L. Griscom 4296* (GH): inlet into Rainy Pond, back of Sand Bridge, 15 July 1940, *M. L. Fernald and B. Long 12238* (GH, NY).

connate forming a pyramidal structure (Figure 3), and with a relatively short free portion much exceeded in length by the anthers. The anthers of *H. morsus-ranae* are oval, approximately as long as wide and ca. 1.0 mm long, while the anthers of *L. spongia* are elongate, much longer than wide and ca. 3.5 mm in length (Figure 3.).

The styles of *H. morsus-ranae* are usually 6 in number, bifid for one half of their length, ca. 4.0 mm long, and much shorter than the petals. The styles of *L. spongia* on the other hand, are 6–9 in number, bifid nearly to the base, 10 15 mm long, and exceeding the petals in length.

Although these floral features are conclusive in separating the two species, their usefulness is limited by the fact that flowering material is often not available. This is especially true of the floating-leaved form of *L. spongia* which is without flowers more than 90% of the time based on herbarium specimens examined.

Hotchkiss (1972) noted that the leaves of *Hydrocharis morsus-ranae* resemble the floating form of *Limnobium spongia* but the former have almost no central sponginess. This sponginess is due to aerenchyma (lacunate mesophyll) which is readily observed on the underside of the leaf. Aerenchyma is more extensive in *L. spongia* and the aerenchyma spaces are generally larger (Figures 4, 5, & 6, Table 3). The emergent leaves of *L. spongia* are usually without aerenchyma, but are not likely to be confused with leaves of *H. morsus-ranae* because of their truncate bases (Figure 7).

In addition to the difference in the size of aerenchyma spaces, the leaves of *H. morsus-ranae* tend to have relatively longer basal lobes (Figure 7). This is readily apparent when leaf lobe length is expressed as a ratio of leaf length (Figure 4, Table 3).

There are also differences in leaf venation between these two species. *Limnobium spongia* tends to have the primary veins on either side of the midvein more ascending while in *Hydrocharis morsus-ranae* these veins tend to be more widely curving, often forming an angle of 80° or 90° with the midvein at the leaf base

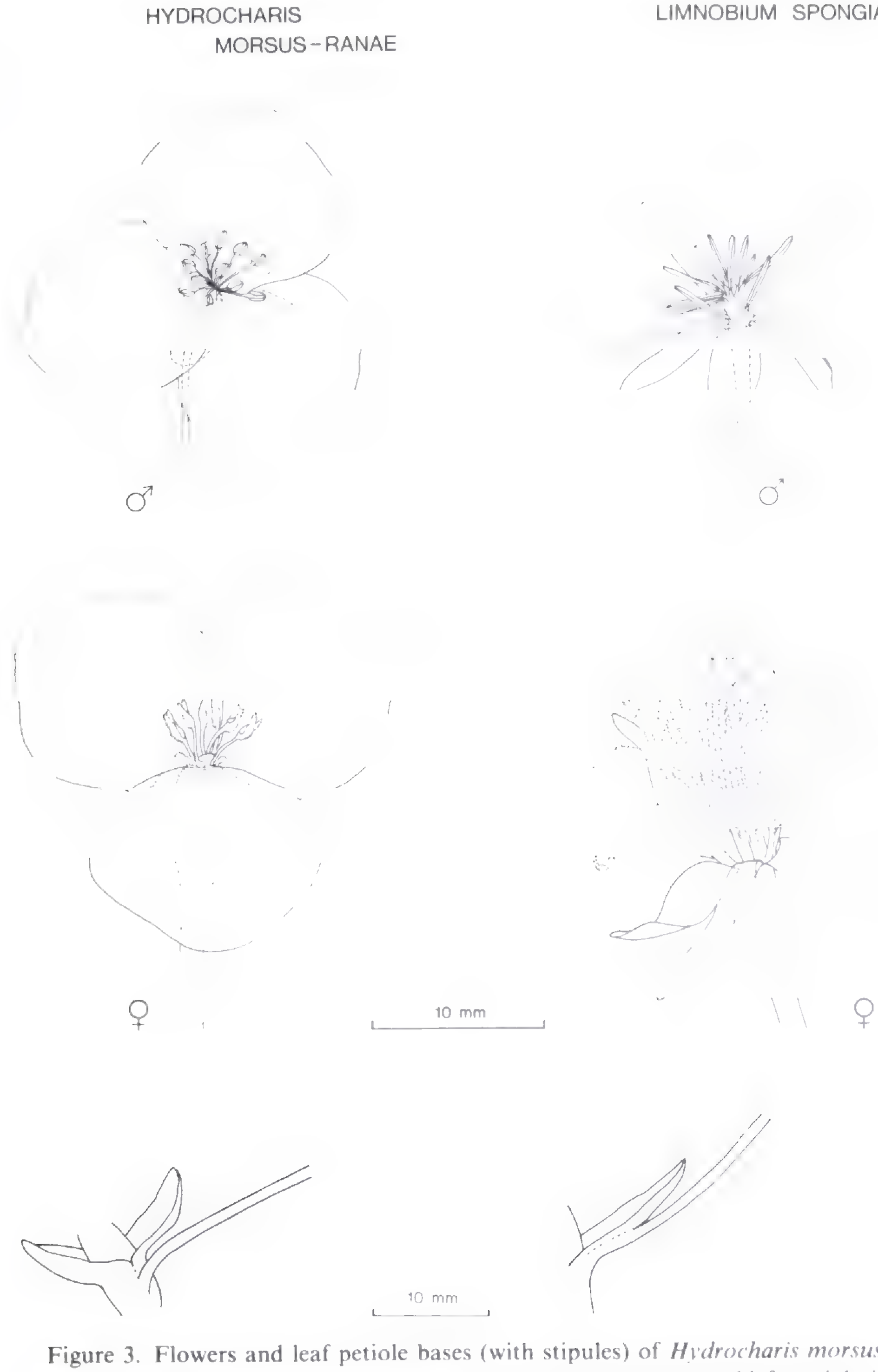

Figure 3. Flowers and leaf petiole bases (with stipules) of *Hydrocharis morsus-ranae* (left) and *Limnobium spongia* (right). From top to bottom (and left to right in brackets), male flowers (Ontario, *Dore 21280*, DAO and Florida, *Chapman*, GH), female flowers (Ontario, *Dore 21717*, DAO and Texas, *Mitchell 4057*, NY) and petiole bases (Ontario, *Catling 3279*, DAO and Kentucky, *Catling 3097*, DAO).

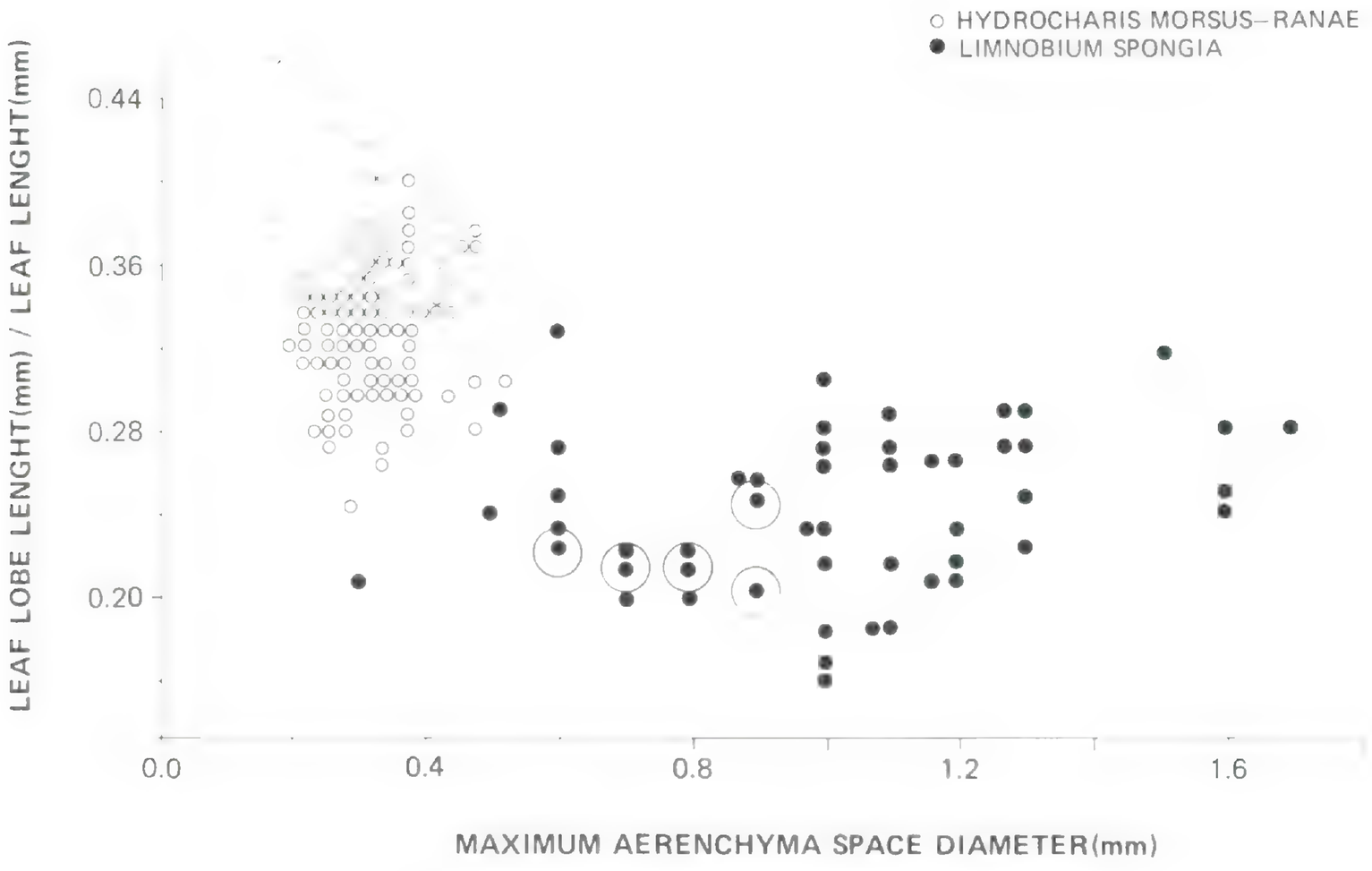

Figure 4. Aerenchyma space diameter plotted against the ratio of leaf lobe length leaf length for *H. morsus-ranae* (including 55 specimens from Europe and 46 from Canada) and *L. spongia* (including 49 specimens from the eastern United States). More than half of the *H. morsus-ranae* had flowers but the only *L. spongia* specimens with flowers are represented by the five encircled dots.

Figure 5. *Hydrocharis morsus-ranae*. Leaf viewed from below (left) and stolon buds (right). Rideau River, Merrickville, Lanark Co., Ontario, 24 Aug. 1965, *W. G. Dore 21790* and *C. Crompton* (DAO).

Figure 6. *Limnobium spongia*. Leaf viewed from below (left) and stolon bud (right). Sumter Wildlife Management area, Sumter Co., Florida, 13 Aug. 1958, *R. Kral 7869* (GH).

Table 3.
Leaf character data.

Minimum, maximum, mean, standard error (SE) and standard deviation (SD) for four leaf characters in *Hydrocharis morsus-ranae* from Europe (HME, n = 55), *H. morsus-ranae* from Canada (HMC, n = 46) and *Limnobium spongia* from eastern United States (LS, n = 49)

	MIN./MAX.	MEAN	SE	SD
1. Arenchyma space diameter (mm)				
HME	0.160 0.480	0.319	0.011	0.081
HMC	0.220 0.540	0.353	0.010	0.065
LS	0.300 1.700	1.016	0.045	0.315
2. Leaf length (mm)				
HME	12.000 45.000	28.725	0.886	6.573
HMC	15.500 42.800	26.922	0.879	5.962
LS	13.000 57.000	28.598	1.480	10.360
3. Leaf lobe length (mm)				
HME	3.300 15.000	9.675	0.334	2.477
HMC	5.000 17.000	9.359	0.369	2.502
LS	2.400 16.000	7.202	0.452	3.164
4. Lef lobe length leaf length				
HME	0.275 0.462	0.336	0.005	0.038
HMC	0.272 0.423	0.346	0.005	0.034
LS	0.167 0.339	0.247	0.006	0.039

(Figure 7). The secondary venation also frequently differs. In *L. spongia* there is usually much more secondary venation parallel to the primary venation and this secondary venation is essentially oriented either parallel or perpendicular to the primary venation. In *H. morsus-ranae* there is less secondary venation parallel to the primary venation and much of it is neither parallel nor perpendicular, but rather diagonal and/or circular or wavy (Figure 8). The very young and earliest-produced floating leaves of *L. spongia*, however, may be very similar to mature leaves of *H. morsus-ranae* in their secondary venation.

Although *Hydrocharis morsus-ranae* does not have a mud form with truncate based leaves like *Limnobium spongia* (see Figure 7,) it does occasionally produce leaves which rise out of the vegetation mat, especially in dense colonies of mature plants. Thus both species can be said to have either floating or emergent leaves. Although

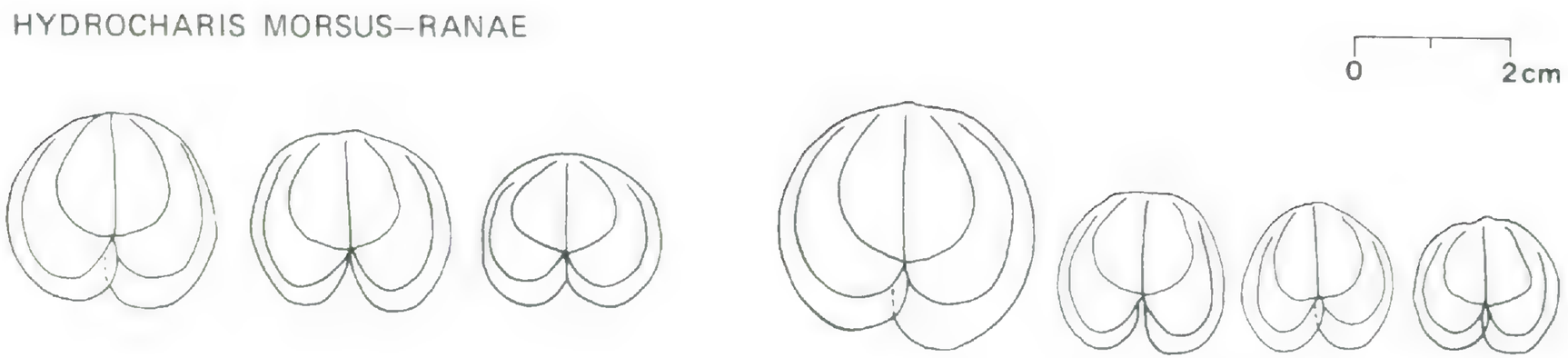

Figure 7. Variation in the leaves of *H. morsus-ranae* (Canada) and *L. spongia* (United States) made from direct tracings.

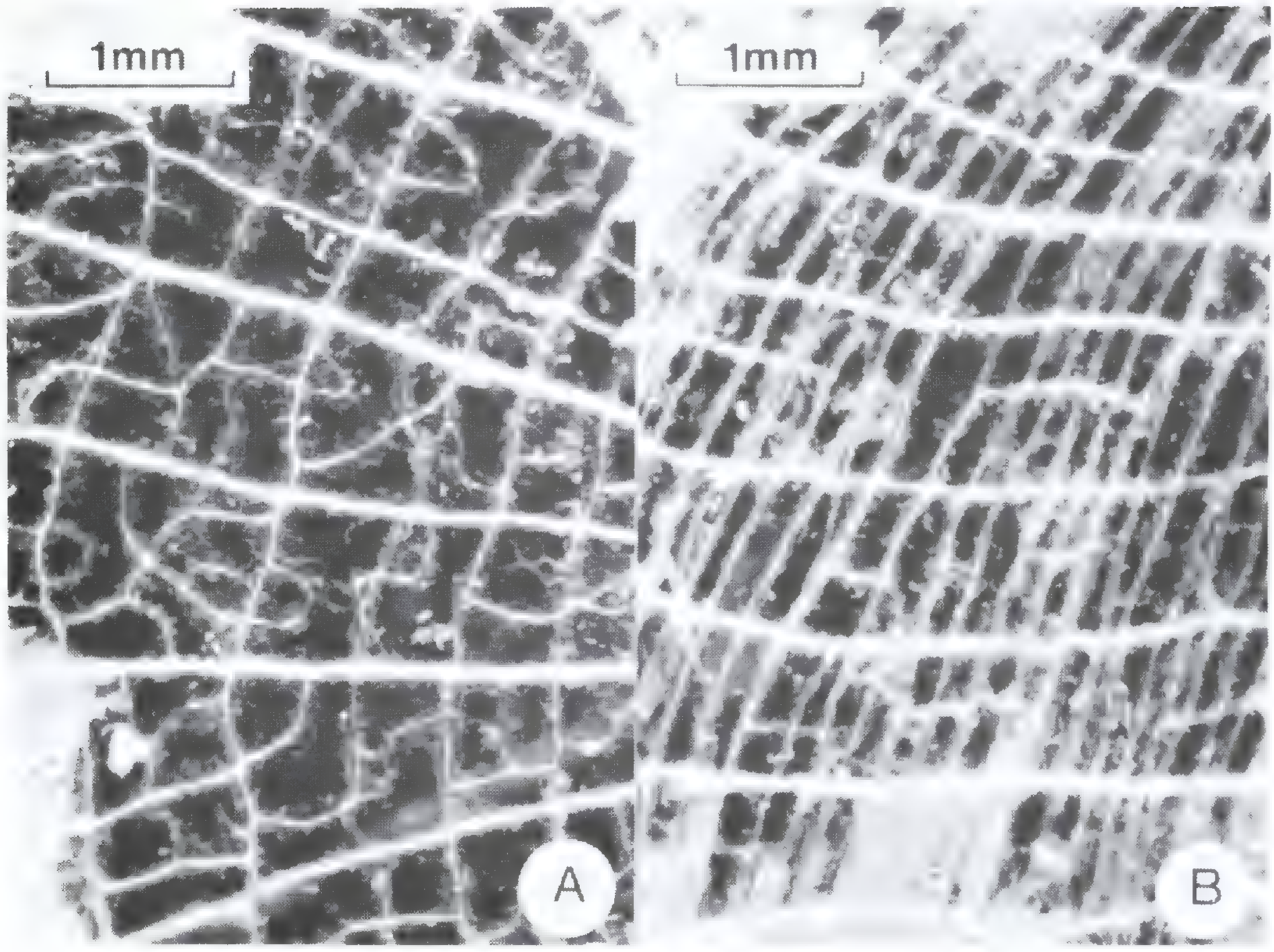

Figure 8. A, *Hydrocharis morsus-ranae* and B, *Limnobium spongia* showing leaf venation between first and second primary lateral veins (A, near Wressell, East Yorkshire, England, *J. Beanland* (T. W. Edmondson herb., NY); B, Delaware City, Delaware, 1 Sept. 1880, *C. Culbert* (A. Commons herb., NY)).

young floating plants of *L. spongia* tend to have relatively longer leaf petioles than *H. morsus-ranae,* there is much overlap in this character.

Hydrocharis morsus-ranae has two lateral stipules free from the leaf petiole base while *Limnobium spongia* has a single stipule adnate to the leaf petiole base (Figure 3). This is a very useful character in living material, but is much more difficult to assess in dried herbarium material.

Both *Hydrocharis morsus-ranae* and *Limnobium spongia* are stoloniferous, the short erect stems producing lateral stolons which travel for some distance below the surface of the water or soft mud and produce terminal buds which develop into new rosettes. The turions of *H. morsus-ranae* are modified overwintering stolon buds. *Limnobium spongia* also produces stolon buds. The stolon buds of *H. morsus-ranae* develop a single root initially and differ in this respect from stolon buds of *L. spongia* which produce numerous roots simultaneously from the base (Figures 5 and 6).

Another consistent and useful difference is observed in the roots. Those of *H. morsus-ranae* are usually unbranched (Sculthorpe, 1967, p. 190; Dore, 1968a), while roots of *L. spongia* usually have numerous simple branches.

Although *Hydrocharis morsus-ranae* often flowers, it rarely develops fruit in certain parts of its range (Sculthorpe, 1967, p. 319) and fruit production may be irregular. Fruit and seeds are developed in some Canadian populations (*e.g.:* St. Anne de Bellevue, 28 Aug. 1961, *D. E. Swales* (DAO)), but their apparent scarcity in the field and in herbarium specimens make them of limited value in identification. The floating-leaved form of *Limnobium spongia*, which is most likely to be confused with *H. morsus-ranae*, apparently possesses flowers and fruit rarely (less than 10%, based on examination of herbarium material). Although the fruiting structures are similar in many respects, the seeds of the two species appear to be quite different. Because of their limited value in identification (due to scarcity) and because of the relatively small sample available (preventing comparisons on a broad geographical basis), these differences have not yet been studied quantitatively. Seeds and illustrations of seeds of *H. morsus-ranae* that have been examined had a minutely tuberculate, rough, ridged and/or slightly winged surface while those of *L. spongia* are echinate with spines about 0.3mm long.

The salient differences between the two species in the characters discussed above have been summarized in Table 4.

ACKNOWLEDGEMENTS

We appreciate the helpful communications of several field botanists and herbarium curators (see text), particularly C. D. K. Cook, H. M. Dale, H. S. Forest, A. Legault, and F. M. Uhler. R. Athey kindly assisted with field study of *L. spongia* in western Kentucky and A. E. Garwood participated in Ontario field study of *H. morsus-ranae*. Finally we appreciate the helpful criticisms of R. L. Stuckey.

Table 4.

Selected comparisons between Hydrocharis morsus-ranae and Limnobium spongia.

	H. morsus-ranae	**L. spongia**
ROOTS	usually unbranched	branched
STOLON BUDS	developing a single root initially at base	with numerous roots developing simultaneously at base
LEAVES		
(a) acrenchyma (visible on lower leaf surface)	larger spaces confined to immediate region of mid-vein, those 1 mm from midvein 0.1-0.5 mm across	extensive, larger spaces 1 mm from midvein 0.4-1.6 mm across
(b) Leaf lobe length (mm)/leaf length (mm)	0.26-0.41	0-0.32
(c) primary veins on either side of midvein	basally forming an angle of 75–90° with the midvein and broadly curving	basally forming an angle of about 30–80° with the midvein and ascending
(d) leaf stipules	two free stipules	single adnate stipule
FLOWERS		
(a) petals	more than 1½ times as long as sepals	less than 1½ times as long as sepals
(b) stamens	9–12, with long free filaments not obviously connate above base	3–12, with filaments largely connate forming a pyramidal structure
(c) anthers	oval, approximately as long as wide, *ca.* 1.0 mm long	elongate, much longer than wide, *ca.* 3.5 mm long.
(d) styles	6, bifid for less than ½ of their length, ca. 4 mm long, much shorter than perianth	6–9, bifid nearly to the base, 10–15 mm long, exceeding perianth.
SEEDS	minutely tuberculate, or muricate or merely with a rough somewhat ridged or winged surface	echinate, the spines to 0.3 mm long.

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A NEW STATION FOR LISTERA AURICULATA (ORCHIDACEAE) IN NEW YORK STATE[1]

JERRY L. PLATT, ELIZABETH YANUCK-PLATT
AND CHARLES J. SHEVIAK[2]

The auricled twayblade, *Listera auriculata* Wiegand, is believed to be rare throughout its range and is currently under review for listing under the provisions of the 1973 Endangered Species Act (U.S. Fish and Wildlife Service, 1980). An essentially Canadian plant, the species ranges from the Maritime Provinces to the Lake Superior region; its southern limits in the U.S. are poorly known and in need of clarification if the species is to be properly treated under the terms of the Act. The principal works on the flora of the northeast and its orchids variously have cited the plant from New York (Morris & Eames, 1929; Fernald, 1950), tentatively reported it from the state (Gleason & Cronquist, 1963), or omitted the state from the species' range (Correll, 1950; Gleason, 1952; Luer, 1975). *Listera auriculata* has been known in New York from a single collection made over 50 years ago on the Tug Hill Plateau in Lewis County (27 June 1927, *N. Hotchkiss 2453*, NYS). Despite rather precise locality information augmented by the recollections of Hotchkiss (letter to Sheviak, February 1980), recent intensive searches have failed to relocate the population. Our recent discovery of a second population of the species in New York consequently is significant.

Listera auriculata typically occurs in alluvial sites along streams, commonly growing in open thickets of *Alnus* and *Betula pumila*, often in freshly deposited sand (Case, 1964; Whiting & Catling, 1977). Such habitat is poorly represented at the Tug Hill locality, where the species reportedly occurred in "rich mucky woods" (Hotchkiss, 1932). The failure of repeated attempts by Sheviak and his colleagues at the State Museum to locate the plant and the paucity of prime habitat at this locality led Sheviak to redirect his attention to the Adirondacks. In this region, apparently suitable

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[2]Requests for reprints should be addressed to Dr. Sheviak

habitat is very abundant, yet poorly studied, thus suggesting that the plant might occur there unnoticed.

In July, 1980, while conducting a survey for The Nature Conservancy along the upper Hudson River in Warren County, the Platts observed and photographed a fruiting *Listera*. Upon subsequent study of the photograph, Sheviak tentatively determined the plant as *Listera auriculata*, a determination based in large part on the riparian nature of the habitat and associated species. On 10 and 16 June 1981, we revisited the site to confirm the identification and found a colony of about 80 plants, of which 12 were in flower. The plants occur along a narrow strip of cobbly-sandy riverbank within the floodplain of the Hudson River, at the base of a northwest-facing slope. The community in which they occur is kept open by ice scouring which annually eliminates tree saplings and coppices scattered *Alnus*. The colony, within a few feet of the river, is overtopped by a fringe of *Tsuga canadensis* and *Fraxinus americana* from the adjacent slope. The *Listera* grow in open sand and mats of *Mnium* sp. and *Rhacomitrium* sp. (?) and frequently protrude through beds of water-deposited debris. The community is dominated by a dense stand of *Osmunda claytoniana; Alnus* growth is particularly suppressed in this area. Associated species include *Impatiens capensis, Maianthemum canadense, Veratrum viride, Thalictrum polygamum, Sanguisorba canadensis, Aster praealtus, A. acuminatus, Anemone canadensis, Sanicula marilandica, Luzula campestris, Carex* sp., and grasses. The colony is centered on a strip of riverbank receiving moisture from a small seep; although the *Listera* is scattered beyond this zone, the perennial seepage may promote the species' survival during abnormally warm or dry periods at this southern locality.

The abundance of apparently suitable habitat in the Adirondacks suggests that the species may be more widespread, and further searching may reveal additional colonies of this small, inconspicuous plant.

An initial collection of a single flowering plant *(Platt 81–28)* and a subsequent collection of individual flowers from a series of plants *(Sheviak 2019)* are deposited at NYS.

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THE 1982 JESSE M. GREENMAN AWARD

The 1982 Jesse M. Greenman Award has been won by Walter S. Judd for his publication "A monograph of *Lyonia* (Ericaceae)" (Jour. Arnold Arbor. **62:** 63–209; 315–436. This monographic study is based on a Ph.D. dissertation from the Department of Biology, Harvard University.

The Greenman Award, a cash prize of $250, is presented each year by the Missouri Botanical Garden. It recognizes the paper judged best in vascular plant or bryophyte systematics based on a doctoral dissertation which was published during the *previous* year. Papers published during *1982* are now being considered for the 16th annual award, which will be presented in the summer of 1983. Reprints of such papers should be sent to: Greenman Award Committee, Department of Botany, Missouri Botanical Garden, P.O. Box 299, St. Louis, MO 63166–0299, U.S.A. In order to be considered for the 1983 award, reprints must be received by 1 July 1983.

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INDEX FOR VOLUME 84

New scientific names are in **bold face.**

Additional records of Hickories in northern New England. 304–305
Additional taxonomic and nomenclatural notes on ferns. 125–130
Alabama. A new Clematis from northeastern, 285–291
Alpine flora of Western Brook Pond and Deer Pond areas, Gros Morne National Park, Checklist of the, 101–115
Amelanchier. II: Do the taxa in the genus Amelanchier form an agamic complex? Experimental taxonomy in the genus, 85–100
Announcements – Meetings
AIBS 33rd meeting inside back cover, No. 838
Field meeting, NE section of Botanical Society of America inside back cover, No. 837
Joint meeting of Northeastern section of Botanical Soc. of America, Torrey Bot. Club, & Philadelphia Bot. Club. inside back cover, No. 838
Announcements of Greenman Awards–
1981 Jesse M. Greenman Award. 157
1982 Jesse M. Greenman Award. 551
Another alien in the California flora. 53–154

Book review: Illustrations of Pteridophytes of Japan. 451
Books received and literature for New England botanists. 314–315
Bremer, Kåre *see* Howard, Richard
Bryophytes of the Flume, Franconia State Park, N.H. 149–152

California flora. Another alien in the, 149–154
Campyloneurum anetioides, *comb. nov.* 125; **C. occultum,** *comb. nov.* 125; **C. pascoense,** *comb. nov.* 125
Carex livida var. grayana and Dryopteris fragrans in Washington County, Vermont. New stations for, 155–156
Catling, P. M., & W. G. Dore. Status and identification of Hydrocharis morsus-ranae and Limnobium spongia in northeastern North America. 523–545
Cheilanthes purpusii (Adiantaceae), a new species from San Luis Potosi, Mexico. 293–295
Cheilanthes purpusii, *sp. nov.* 293, fig. 294
Chromosome numbers of Peruvian Compositae. 131–137
Clematis socialis, *sp. nov.* 287, fig. 286
Composition, seasonal occurrence, and reproductive periodicity of the Phaeophyceae (Brown Algae) in New Hampshire. The. 411–437
Connecticut. A short-lived addition to the flora of, 305–307
Connecticut flora. Psilocarya scirpoides Torr., an addition to the, 307–309
Ctenitis honesta, *comb. nov.* 127, **C. Tonduzii,** *comb. nov.* 127, **C. velata,** *comb. nov.* 127

Dennstaedtiaceae tribe **Monachosoreae,** *comb. nov.* 126
Dillon, Michael, & B. L. Turner. Chromosome numbers of Peruvian Compositae. 131–137
Diplazium lilloi, *comb. nov.* 127
Dore, W. G. *see* Catling, P. M.
Dryopteris fragrans in Washington County, Vermont. New stations for Carex livida var. grayana and, 155–156
Dryopteris Tsingiana, *comb. nov.* 126
Dumond, D. M. *see* Eastman, L. M.

Eastman, L. M., R. L. Hinkle, & D. M. Dumond. A new station of Goodyera oblongifolia Raf. in northern Maine. 309–313

Experimental Taxonomy in the genus Amelanchier. II: Do the taxa in the genus Amelanchier form an agamic complex? 85–100

Fagbemi, B. O. B., & J. K. Morton. Studies on Mentha × dumetorum Schult. (Labiatae) to confirm its presumed parentage — M. aquatica Linn. × M. longifolia (Linn.) Huds. 439–445

Glime, Janice M. Bryophytes of the Flume, Franconia State Park, N.H. 149–152

Golden Clubs. The Provincelands, 297–300

Goodyera oblongifolia Raf. in northern Maine. A new station of, 309–313

Grammitis achilleifolia, *comb. nov.* 128; **G. gradata,** *comb. nov.* 128; **G. pozuzoensis,** *comb. nov.* 129; **G. rostrata,** *comb. nov.* 129; **G.** section **Cryptosorus,** *comb. nov.* 128; **G.** sect. **Glyphotaenium,** *stat. nov.* 128; **G.** sect. **Pleurogramme,** *comb. nov.* 128; **G. venulosa,** *comb. nov.* 129

Gros Morne National Park. Checklist of the alpine flora of Western Brook Pond and Deer Pond areas, 101–115

Hehre, Edward J. *see* Mathieson, Arthur C.

Hickories in northern New England. Additional records of, 304–305

Hill, Steven R. A monograph of the genus Malvastrum A. Gray (Malvaceae: Malveae). 1–83, 159–264, 317–409

Hinkle, R. L. *see* Eastman, L. M.

Howard, Richard, & Kåre Bremer. Olof Swartz in Boston, 1783. 143–148

Hydrocharis morsus-ranae and Limnobium spongia in northeastern North America. Status and identification of, 523–545

Index to Volume 84, Nos. 837–840 (1982). 553–559

Judd, Walter S. The taxonomic status of Oxypolis greenmanii (Apiaceae). 265–279

Kral, Robert. A new Clematis from northeastern Alabama. 285–291

La Duke, John C. A new species of Tithonia (Compositae) and infrageneric classification. 139–141

La Duke, John C. Revision of Tithonia. 453–522

LeBlond, Richard. The Provincelands Golden Clubs. 297–300

Limnobium spongia in northeastern North America. Status and identification of Hydrocharis morsus-ranae and, 523–545

Listera auriculata (Orchidaceae) in New York State. A new station for, 547–549

Literature for New England botanists. 452

Losphosoria quadripinnata var. **contracta,** *comb. nov.* 126

Maine. A new station of Goodyera oblongifolia in northern, 309–313

Maine, with some comments on a unique floral form. New locations for Podostemum ceratophyllum Michx. (Podostemaceae) in New Hampshire and, 301–303

Malvastrum A. Gray (Malvaceae: Malveae). A monograph of the genus, 1–83, 159–264, 317–409

Malvastrum 1–83. Chromosome Nos. 69–70; comparative morphology 38; distribution & habitat 16, map 17; ethnobotany 29; literature and historical survey 4; phenology and reproductive biology 30, table of pollinators and predators 37; phylogeny 70; pollen figs. 59, 61; Wagner tree 76.

Malvastrum 159–264. Key to taxa 168. Sections: **Amblyphyllum,** *sect. nov.* 251; **Americanum,** *sect. nov.* 186; **Interruptum,** *Sect. nov.* 175; **Sidopsis,** *comb. et stat. nov.* 169; **Tomentosum,** *sect. nov.* 211. Species: M. amblyphyllum 258; americanum var. americanum 187, var. stellatum 201; bicuspidatum subsp. bicuspidatum 232, subsp. campanulatum 239, subsp. oaxacanum 242, subsp. tumidum var. glabrum 249 & var. tumidum 244; chillagoense 205; grandiflorum 251; guatemalense 228; hispidum 169; interruptum 180; scoparioides 220; spiciflorum 175; tomentosum subsp. pautense 218, subsp. tomentosum 211. summary of taxa 168; taxonomic treatment 159

Malvastrum 317–409. Data matrices (App. II) 364. Excluded or uncertain species (App. III) 372. Sections: **Corchorifolium,** *sect. nov.* 348; **Malvastrum,** *emend.* 317. Species: M. aurantiacum 318; coromandelianum subsp. coromandelianum 324, subsp. capitatospicatum 339, subsp. fryxellii 343; corchorifolium 348. Summary of distribution (App. I) 362

Manning, Wayne E. A new record of Scarlet Oak in southwestern New Hampshire. 156

Manning, Wayne E. Additional records of Hickories in northern New England. 304–305

Mathieson, Arthur C., & Edward J. Hehre. The compositon, seasonal occurrence, and reproductive periodicity of the Phaeophyceae (Brown Algae) in New Hampshire. 411–437

Mehrhoff, Leslie J. A short-lived addition to the flora of Connecticut. 305–307

Mehrhoff, Leslie J. Psilocarya scirpoides Torr., an addition to the Connecticut flora. 307–309.

Mentha × dumetorum Schult. (Labiatae) to confirm its presumed parentage — M. aquatica × M. longifolia (Linn.) Huds. Studies on. 439–445

Mexico. Cheilanthes purpusii (Adiantaceae), a new species from San Luis Potosi. 293–295

Microgramma crispata, *comb. nov.* 129; **M. geminata,** *comb. nov.* 129; **M. rosmarini-folium,** *comb. nov.* 129

Morton, J. K. *see* B. O. B. Fagbemi

Nesom, Guy L., & Tod F. Steussy. Nesting of beetles and ants in Clibadium microcephalum S. F. Blake (Compositae: Heliantheae) 117–124

New Clematis from northeastern Alabama. A. 285–291

New England. Additional records of Hickories in northern, 304–305

New England Notes:

Additional records of Hickories in northern New England. 304–305

A new record of Scarlet Oak in southwestern New Hampshire. 156

A new station of Goodyera oblongifolia Raf. in northern Maine. 309–313

A short-lived addition to the flora of Connecticut. 305–307

New locations for Podostemum ceratophyllum Michx. (Podostemaceae) in New Hampshire and Maine, with some comments on a unique floral form. 301–303

New stations for Carex livida var. grayana and Dryopteris fragrans in Washington County, Vermont. 155–156

Psilocarya scirpoides Torr., an addition to the Connecticut flora. 307–309

The Provincelands Golden Clubs. 297–300

Nesting of beetles and ants in Clibadium microcephalum S. F. Blake (Compositae: Heliantheae). 117–124

New Hampshire and Maine, with comments on a unique floral form. New locations for Podostemum ceratophyl-

lum Michx. (Podostemaceae) in, 301–303
New Hampshire. A new record of Scarlet Oak in southwestern, 156
New Hampshire (as N. H.). Bryophytes of the Flume, Franconia Notch State Park, 149–152
New Hampshire. The composition, seasonal occurrence, and reproductive periodicity of the Phaeophyceae (Brown Algae) in, 411–437
New locations for Podostemum ceratophyllum Michx. in New Hampshire and Maine, with comments on a unique floral form. 301–303
New record of Scarlet Oak in southeastern New Hampshire. A, 156
New species of Tithonia (Compositae) and infrageneric classification. A, 139–141
New station for Listera auriculata (Orchidaceae) in New York State. A, 547–549
New station for Goodyera oblongifolia Raf. in northern Maine. A, 309–313
New stations for Carex livida var. grayana and Dryopteris fragrans in Washington County, Vermont. 155–156
New York state. A new station for Listera auriculata (Orchidaceae) in, 547–549
North America. Status and identification of Hydrocharis morsus-ranae and Limnobium spongia in northeastern, 453–522
North Carolina. Octoploid populations of Oenothera fruticosa L. (Onagraceae) from coastal, 281–283
Note on the occurrence of root-shoots in Vaccinium corymbosum L. A, 447–450
Notice of (series) Publication: Evolutionary Monographs. inside back cover, No. 839
Octoploid populations of Oenothera fruticosa L. (Onagraceae) from coastal North Carolina. 281–283
Oenothera fruticosa L. (Onagraceae) from coastal North Carolina. Octoploid populations of, 281–283
Olof Swartz in Boston, 1873. 143–148
Oxypolis filiformis ssp. **greenmanii,** *comb. et stat. nov.* 277
Oxypolis greenmanii (Apiaceae). The taxonomic status of, 265–279

Paesia bivalvis, *comb. nov.* 127
Peruvian Compositae. Chromosome numbers of, 131–137
Phaeophyceae 411–437. Annotated checklist 423; Tables: collection sites 412, seasonality, reproductive periodicity, longevity, & distribution 419
Phaeophyceae (Brown Algae) in New Hampshire. The composition, seasonal occurrence, and reproductive periodicity of the, 411–437
Philbrick, C. Thomas. New locations for Podostemum ceratophyllum Michx. (Podostemaceae) in New Hampshire and Maine, with some comments on a unique floral form. 301–303
Platt, Jerry L., Elizabeth Yanuck-Platt, & Charles J. Sheviak. A new station for Listera auriculata (Orchidaceae) in New York state. 547–549
Pleopeltis Conzattii, *comb. nov.* 129; **P. fuscopunctata,** *comb. nov.* 129
Podostemum ceratophyllum Michx. (Podostemaceae) in New Hampshire and Maine, with comments on a unique floral form. New locations for, 301–303
Polypodiaceae tribe **Loxogrammeae,** *stat. nov.* 129
Provincelands Golden Clubs. The, 297–300
Psilocarya scirpoides Torr., an addition to the Connecticut flora. 307–309

Reeves, Timothy. Cheilanthes purpusii (Adiantaceae), a new species from San Luis Potosi, Mexico. 293–295
Revision of Tithonia. 453–522
Roberts, B. A. *see* Robertson, Alexander

Robertson, Alexander, & B. A. Roberts. Checklist of the alpine flora of Western Brook Pond and Deer Pond areas, Gros Morne National Park. 101–115
Robinson, W. Ann. Experimental taxonomy in the genus Amelanchier. II: Do the taxa in the genus Amelanchier form an agamic complex? 85–100
Rollins, Reed C. Another alien in the California flora. 153–154
Root-shoots in Vaccinium corymbosum L. A note on the occurrence of. 447–450

Saccoloma ferulaceum, *comb. nov.* 127
San Luis Potosi, Mexico. Cheilanthes purpusii (Adiantaceae), a new species from. 293–295
Sheviak, Charles J. *see* Platt, Jerry L.
Short-lived addition to the flora of Connecticut. A. 305–307
Statement of ownership. inside back cover, No. 840
Status and identification of Hydrocharis morsus-ranae and Limnobium spongia (Hydrocharitaceae) in northeastern North America. 523–545
Steussy, Tod F. *see* Nesom, Guy L.
Straley, Gerald B. Octoploid populations of Oenothera fruticosa (Onagraceae) from coastal North Carolina. 281–283
Studies on Mentha × dumetorum schult. (Labiatae) to confirm its presumed parentage — M. aquatica Linn. × M. longifolia (Linn.) Huds. 439–445

Taxonomic status of Oxypolis greenmanii (Apiaceae). The. 265–279
Thelypteris subgenus **Parathelypteris,** *stat. nov.* 128; **T. brachypus,** *comb. nov.* 128; **T. lugubris,** *comb. nov.* 128
Tithonia (Compositae) and infrageneric classification. A new species of. 139–141
Tithonia, Revision of. 453–522. Concepts of species, varieties, and sections 460; cytology 457, table of chromosome nos. 458; distribution maps 484, 488, 491, 497, 517; doubtful and excluded taxa 517; generic and subtribal relationships 455; history 454; isolating mechanisms 459; key to the taxa 478; morphology & taxonomic criteria 476; numerical taxonomy 460; table of characters used 462; phylogenetic reconstruction 469, data matrix for 473, table of characters used 472; taxonomic treatment 478; Tithonia brachypappa 485; calva 506, var. **auriculata,** *comb. et stat. nov.* 509, var. calva 507, var. lancifolia 510; diversifolia 498; fruticosa 501; hondurensis 514; koelzii 495; longiradiata 511; pedunculata 504; rotundifolia 480; sect. Mirasolia 506; sect. Tithonia 480; series Fruticosa 501; ser. Grandiflorae 494; ser. Tithonia 480; thurberi 492; tubaeformis 488
Tithonia series **Grandiflorae,** *ser. nov.* 140; ser. **Fruticosae,** *ser. nov.* 140; section *Mirasolia, stat. nov.* 141; **hondurensis,** *sp. nov.* 139
Tryon, Alice F. *see* Tryon, Rolla
Tryon, Rolla, & Alice F. Tryon. Additional taxonomic and nomenclatural notes on ferns. 125–130
Turner, B. L. *see* Dillon, Michael

Vaccinium corymbosum L. A note on the occurrence of root-shoots in. 447–450
Vander Kloet, S. P. A note on the occurrence of root-shoots in Vaccinium corymbosum L. 447–450
Vermont. New stations for Carex livida var. grayana and Dryopteris fragrans in Washington County. 155–156

Yanuck-Platt, Elizabeth *see* Platt, Jerry L.

Zika, Peter F. New stations for Carex livida var. grayana and Dryopteris fragrans in Washington County, Vermont. 155–156

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RHODORA October 1982 Vol. 84, No. 840

CONTENTS

Revision of Tithonia
John C. La Duke 453

Status and Identification of Hydrocharis Morsus-Ranae and Limnobium Spongia (Hydrocharitaceae) in Northeastern North America
P. M. Catling and *W. G. Dore* 523

A New Station for Listera Auriculata (Orchidaceae) in New York State
Jerry L. Platt, Elizabeth Yanuck-Platt, and *Charles J. Sheviak* 547

Jesse M. Greenman Award 551

Index to Volume 84 553

Statement of Ownership . . . . . cover iii